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THE BIOLOGY OF SOME BLACK FLIES (DIPTERA : SIMULIIDAE) OF ALBERTA

by

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ABSTRACT

The biology of 15 simuliid species in northern Alberta was studied. *Simulium vittatum* Zetterstedt and *Simulium venustum* Say were the most abundant; *Prosimulium travisi* Stone and *Prosimulium onychodactylum* Dyar and Shannon were rare. Characteristically the univoltine species (except *Cnephia mutata* Malloch) were autogenous throughout the area. *C. mutata* was represented by both the triploid (parthenogenetic) and the rare diploid sexual forms. A key for the identification of the 31 species reported from Alberta is given. Regular sampling of simuliid larvae in the rivers and creeks shows that there are several peaks of abundance every year (1963-1965) due to the occurrence of the larvae of more than one species in the breeding localities, and that the dates, numbers and composition differ slightly depending on the date of the ice break-up and the march of temperature during each season. The over-wintered larvae of *S. vittatum* were present in the water under the ice. The susceptibility of the larvae to DDT was measured and their migration downstream was investigated by the use of plastic sampling cones. The infection rates of the adults and aquatic stages by nematodes and microsporidian protozoans and an evaluation of both predators and parasites as control agents are given.

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LITERATURE REVIEW

The family Simuliidae was erected by Rondani in 1856 (Stirps LXVI Simulina Dipterologia Italica, p. 175).

Numerous accounts of suffering due to the biting of black flies in North America are found in, for example, Champlain 1599 (in Biggar 1922 and 1925), Gabriel Sagard 1631, Garry 1900 and (Father) Le Jeune (in Kenton, 1925) and Lahontan 1703. Louis Agassiz's account of his trip (1850) along the shores of Lake Superior gives a vivid picture of the attacks of black flies.

Lugger 1896 and Riley 1887 started the regional listing of the simuliids in the United States, followed by Johannsen 1903, Forbes 1912, Emery 1913, Malloch 1914 and Jobbins-Pomeroy 1916.

Edwards (1915) and Enderlein (1931) started the work on the systematics of the family utilizing species from all zoogeographical regions.

Cameron (1913, 1922) reported on the black flies of Saskatchewan and described Simulium simile (= arcticum) in greater detail. Hearle (1932) described the black flies of British Columbia. Twinn (1936) reported on the classification and distribution of black flies of eastern Canada. Davies (1950, 1951, 1952, 1957, 1958, 1959, 1961) and Davies and Peterson (1956, 1957) studied the ecology and life history of black flies in Ontario. Hocking and Pickering (1954) and Hocking and Richards (1952) studied black flies in northeastern Canada. Shewell (1952, 1955, 1958) reported on the arctic and subarctic simuliids. Fredeen (1958) and

Fredeen and Shemanchuck (1960) investigated the simuliids of Alberta, Saskatchewan and Manitoba.

Strickland (1938, 1946) recorded eight species of black flies in Alberta; the number is now 31.

In the United States additional regional lists of black flies were published: Western U.S.A. (Stains and Knowlton 1940), Minnesota (Nicholson and Mickel 1950), Alaska (Stone 1952 and Sommerman 1953), Utah (Peterson 1960), New York (Stone and Jamnback 1964).

Ecological and biological studies were included in most of the above papers. The control of black flies using chemicals was started in Canada by Prevost (1947, 1948). Hocking, Twinn and McDuffie (1949) investigated various insecticides. Further reports on this subject were published by Arnason, Brown, Fredeen, Hopewell and Rempel 1949, Brown 1952, 1955, Brown *et al*. 1951, Hocking 1950, 1953, Hocking and Richards 1952, Peterson and Wolfe 1958, Peterson and West 1960, and West, Brown and Peterson 1960.

Cytological studies on black flies commenced with the work of Rothfels and Dunbar in 1953. Additional studies were reported by Rothfels 1956, Dunbar 1958, Basrur and Rothfels 1959, Landau 1962 and Pasternack 1964. The following species have been studied cytologically in North America: *Simulium vittatum* Zetterstedt, *Simulium tuberosum* Lundstroem, *Simulium aureum* Fries, *S. latipes* Mg., *Cnephia mutata* Malloch, *Prosimulium fontanum* Syme and Davies, *Prosimulium hirtipes* Fries, *Prosimulium frohnei* Sommerman, *Prosimulium fulvum* Coquillett, *Prosimulium travisi* Stone, *Prosimulium formosum* Shewell, *Prosimulium fuscum* Syme and Davies, *Prosimulium mixtum* Syme and Davies.

STUDY AREA

FLATBUSH

The Flatbush study area is about 100 miles north of Edmonton (54° 15-54° 50' N, 113° 30-114°, 15' W), and lies within the boreal forest region of central Alberta. The field station was seven miles west of Flatbush village (54° 40' N, 114° 10' W). Smith is 50 miles north of Flatbush, Athabasca town is 40 miles east, and Hinton 200 miles west. All these localities were used as centres during the survey (Fig. 1).

The aspen and spruce forest is intact in long stretches and the cultivated land (farms and pastures) is located away from the rivers. There are no large urban centres (Happold 1965).

Climate and Weather

The long cold winter, characteristic of the continental climate, commences in November and ends in March. The snow melts in April and the ice breaks in the rivers and creeks in April and May. During April the temperature rises to 40°F by day and drops to 20°F by night. In May the temperature reaches 80°F and drops to 35°F at night. The average maximum and minimum temperatures in June are 78°F and 42°F. July and August are warm and the temperature stays above 40°F. In September low temperatures are recorded.

The relative humidity records indicate an overall average of 61%

(40-92%) during the May to September period. The diurnal records show fluctuations of relative humidity especially before sunset and for a short period after sunrise. There seems to be a peak in the morning followed by a drop at noon and a rise in the afternoon which continues well in the night. Temperature (air), relative humidity and rainfall records are tabulated below.

The average date of ice break-up in the Pembina river was April 17 (average of 10 years).

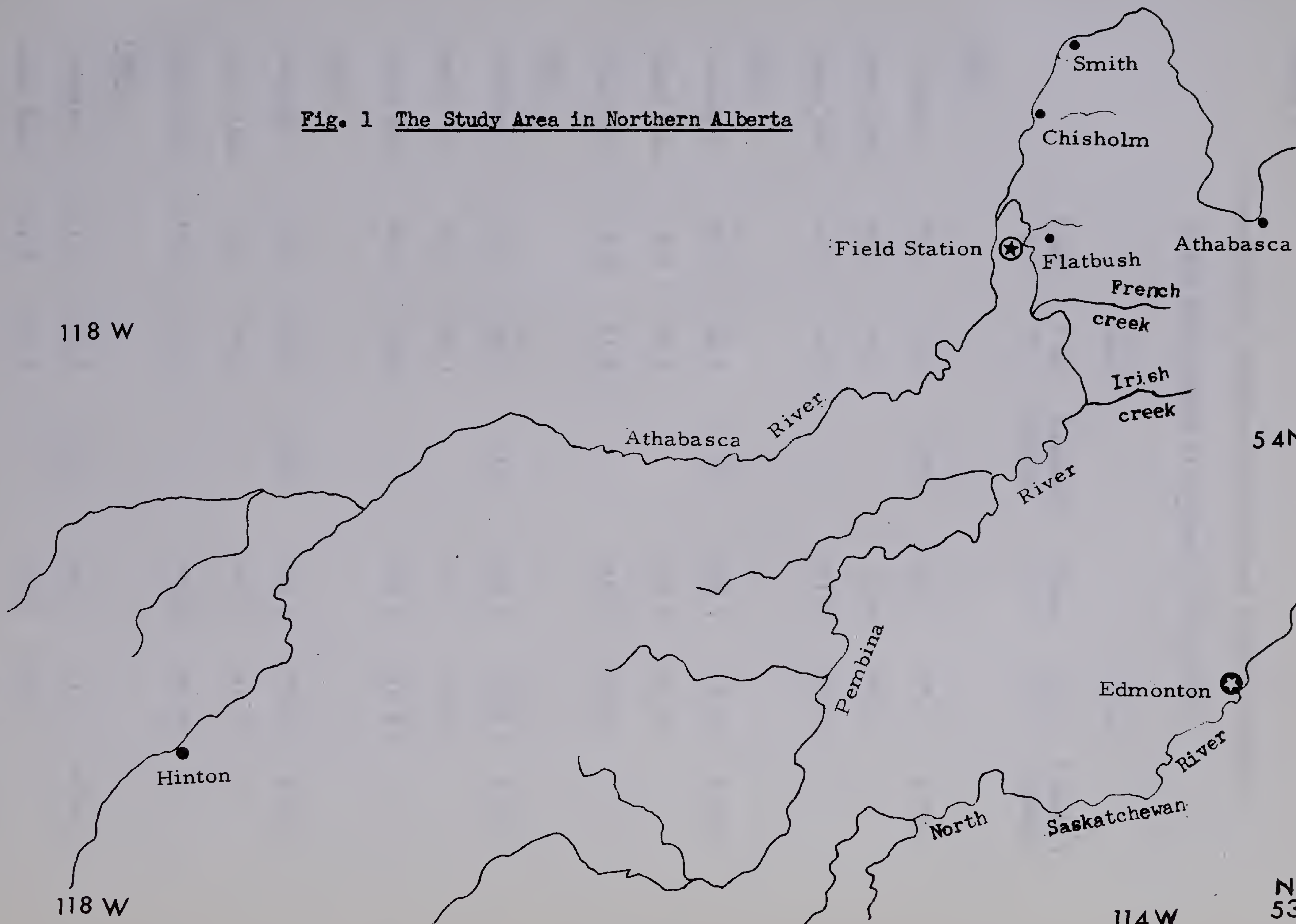
Vegetation

The forest plants include besides aspen and spruce many shrubs such as rose, the cranberry, raspberry and other berries, horsetails and grasses (Happold 1965).

The plants come into leaf in May and by the end of September the herbaceous plant life has ended and the leaves have fallen. The insect population of this area is closely associated with the flora. All the species of black flies were collected feeding or resting on plants.

In the study area in running water very few aquatic plants were encountered. The vegetation near the water is composed of horsetails, mosses, and algae. The banks of the rivers are steep and devoid of vegetation but further away from the river bed the forest is found. The creeks have low banks and the vegetation is dense and in shallow water reaches inside the creek bed. Some of the creeks are shaded thus providing suitable habitats for some black fly species.

Fig. 1 The Study Area in Northern Alberta



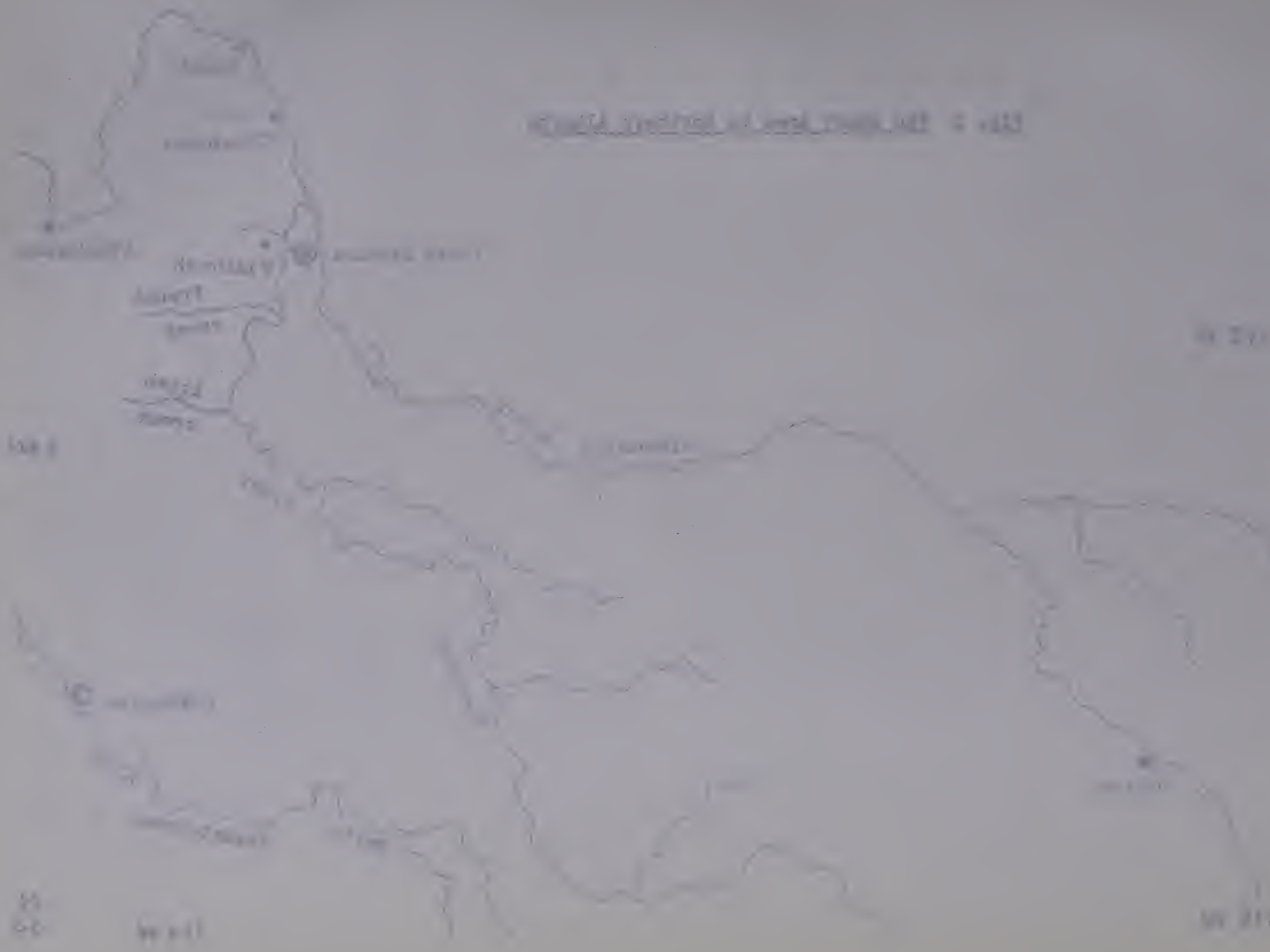


Table 1.

Temperature, relative humidity and rainfall records

in the field station at Flatbush : 1961-1965

	May			June		
	Temp. F.	R.H. %	Rainfall inches	Temp. F.	R.H. %	Rainfall inches
<u>1961</u>						
Average	58.9	63.5	0.30	63.1	68.3	4.49
Mean Max.	66.1	87.4	-	75.0	89.2	-
Mean Min.	41.7	39.7	-	51.3	47.5	-
<u>1962</u>						
Average	50.3	68.2	0.32	58.1	67.5	3.99
Mean Max.	61.8	94.8	-	69.7	93.5	-
Mean Min.	38.8	41.7	-	46.5	43.5	-
<u>1963</u>						
Average	51.2	64.3	1.37	63.2	69.4	2.97
Mean Max.	62.1	92.1	-	67.7	91.5	-
Mean Min.	40.7	40.5	-	43.4	47.8	-
<u>1964</u>						
Average	50.2	65.5	0.94	64.2	70.2	3.24
Mean Max.	62.1	90.0	-	68.3	93.4	-
Mean Min.	41.2	41.7	-	44.6	42.8	-
<u>1965</u>						
Average	51.4	63.5	1.41	62.1	71.1	4.89
Mean Max.	64.5	92.1	-	70.2	93.4	-
Mean Min.	42.6	40.5	-	47.1	49.8	-

Table 1 (cont.)

	July			August			September		
	Temp. F.	R.H. %	Rain-fall "	Temp. F.	R.H. %	Rain-fall "	Temp. F.	R.H. %	Rain-fall "
1961									
Average	62.7	69.9	4.38	64.3	67.2	0.88	58.4	69.9	2.15
Mn. Max.	74.0	89.7	-	77.6	90.0	-	66.5	94.4	-
Mn. Min.	51.4	39.7	-	51.1	42.6	-	40.1	44.8	-
1962									
Average	60.0	72.0	4.08	60.3	72.7	2.49	57.6	74.3	2.01
Mn. Max.	71.0	94.7	-	71.4	94.8	-	67.4	97.8	-
Mn. Min.	49.0	49.3	-	49.2	50.9	-	38.6	57.7	-
1963									
Average	64.1	70.6	3.12	60.2	71.5	0.94	52.4	72.2	1.65
Mn. Max.	70.5	90.8	-	69.4	90.5	-	65.1	93.2	-
Mn. Min.	46.9	48.9	-	46.1	46.6	-	39.2	50.1	-
1964									
Average	65.7	71.5	3.51	62.2	71.3	1.21	59.3	74.1	1.98
Mn. Max.	71.2	91.2	-	70.4	94.4	-	69.1	94.8	-
Mn. Min.	46.9	46.9	-	45.5	48.8	-	39.7	53.3	-
1965									
Average	63.9	72.4	4.74	62.4	75.5	1.21	59.7	77.7	2.11
Mn. Max.	72.1	92.4	-	70.0	90.8	-	64.8	95.5	-
Mn. Min.	49.8	47.8	-	48.2	46.5	-	41.1	54.5	-

Table 2.

List of aquatic plants found in the simuliid breeding sites

Chlorophyceae:	Stigeodonium
	Pediastrum
Fragilariaceae:	Asterionella
Fontinalaceae:	Fontinalis dalecarlica Linn.
Equisetaceae:	Equisetum sp.
Typhaceae:	Typha latifolia Linn.
Sparganiaceae:	Sparganium hyperboreum Laestad
	S. multipendunculatum Morang
Najadaceae:	Potamogeton americanus C. and S.
	P. richardsonii (Benn.) Rybd.
Alismaceae:	Sagittaria australis J. G. Sm.
Butomaceae:	Elodea canadensis (Pursh)
	Vallisneria spiralis Linn.
Pontederiaceae:	Pontederia (cordata Linn. ?)
Ceratophyllaceae:	Ceratophyllum spp.
	(C. demersum Linn. ?)
Cruciferae:	Radicula sp.
Haloragidaceae:	Myriophyllum spicatum Linn.

Rivers and Creeks

Some of this information was kindly provided by the District Engineer, Water Research Branch, Department of Mines and Technical Surveys (Calgary).

The Athabasca River

The drainage area of this river is 29,600 sq. miles. It flows north from the Rocky Mountains and pours into lake Athabasca. The mean discharge in April is 4,700 cubic feet per second, in May 21,200 ft^3/sec, in June 33,000 ft^3/sec, in July 32,000 ft^3/sec, in August 29,200 and in September 25,300 ft^3/sec. The mean velocity increases from 1.8 ft/sec in April to 2.8 ft/sec in June and is nearly uniform in the period June-September. The effects of the rains and melting ice in the mountains are seen in the study area.

The river bed is sandy with coarse gravel but a mud layer is slowly deposited at the end of the June floods. The main stream is devoid of vegetation except for some algal growth on rocks under the water. There is a narrow zone of vegetation at the edge of the water composed of horsetails and reeds.

Due to the gentle slope of the land in the study area there are no rapids in the river but a few isolated riffles are present and *S. arcticum* Malloch and *S. tuberosum* were found breeding in these.

The Pembina River

The drainage area of this river is 4,550 sq. miles. The Pembina

flows north from the Rocky Mountains and conjoins the Athabasca river 10 miles north of Flatbush. From the low discharge of 320 ft^3/sec in April it reaches 2,230 ft^3/sec in May 1,320 ft^3/sec in June and July, 995 ft^3/sec in August and 2,000 ft^3/sec in September. The velocity of the current ranges from less than 1.5 ft/sec in April to more than 2.3 ft/sec in May.

The river banks are steep and the river valley is bare but a fringe of vegetation is present at the edge of the water consisting of horsetails and willows. The stream bed is a mixture of fine sand, clay and gravel. This condition resulted in a better crop of aquatic foliage than in the Athabasca river. The Pembina river has large stretches of riffles which increase at low water level. At low water level algae cover stones and rocks, and their filaments and the stones provide suitable substrates for attachments of the black fly larvae. Seven species of simuliids were found breeding in the Pembina river (*S. arcticum*, *S. tuberosum*, *S. luggeri* Nicholson and Mickel, *S. venustum* Say, *S. vittatum* Zetterstedt, *S. decorum* Walker and *S. latipes*).

Irish Creek

Irish creek crosses highway 44, 65 miles north of Edmonton. It drains the marshes east of the highway and flows into the Pembina river. The creek is about 10 feet wide with steep banks. The water depth ranges from 1 to 3 feet. It flows in part in the shade of forest. The creek is rich in vegetation and although no overwintering larvae were found in it,

the larvae of four species of black fly were collected in May (*Prosimulium decemarticulatum* (Twinn), *Cnephia dacotensis* (Dyar & Shannon), *Cnephia mutata* (Malloch), and *C. emergens* Stone). *Simulium venustum* Say, *Simulium vittatum* Zetterstedt, and *Simulium latipes* (Meigen) were the dominant species later in the season.

French Creek

This creek drains Cross lake and flows west to the Pembina. The creek is up to 18 feet wide and the water is one to two feet deep. The velocity of the current varies from one foot/second to two feet/second near the junction of the creek and the Pembina river. The creek is rich in vegetation especially reeds. The effluence point and the numerous beaver dams provided suitable breeding sites for black flies. The larvae and eggs of six species of black flies were collected. The overwintering larvae of *S. vittatum* were present in water under the ice in 1963, 1964, and 1965.

Cross Lake Creek

This creek flows into Cross lake draining swamps and small lakes north of Cross lake. The creek is eight to ten feet wide but the maximum water depth is one foot. It flows through dense growth of vegetation and is therefore shaded thus providing ideal breeding habitat for *S. decorum*.

Flatbush Creek (Andy's Creek)

This creek flows into the Pembina at Flatbush draining the swamps

east of the village. The creek channel is choked with vegetation in some places, dammed in two places but receives many small rills. Some observations on repopulation of the creek,after damming, by aquatic fauna especially black flies were made.

Chisholm Creek

This creek flows into the Athabasca river at Chisholm (25 miles north of Flatbush). It is dammed near the junction with the Athabasca to provide water for the lumber mills in the village. The creek channel is 15 feet wide and the water depth varies from nine inches to 1.5 feet. The overwintering larvae of _S. vittatum_ were abundant and the highest rates of infestation by parasitic nematodes were recorded here in three consecutive years.

Table 3.

Chemical analysis of water using

Hach Model AL-36-P water analysis kit

	Athabasca River			Pembina R.	Creeks		
pH	Hin-ton	Chis-holm	Atha-basca	Flatbush	Irish	French	Chis-holm
April	-	7.5	7.5	7.5	8.0	8.0	8.0
May	7.5	7.5	7.5	7.5	8.0	8.0	8.0
June	8.0	8.0	8.0	7.5	8.0	8.0	8.0
July	8.0	8.0	8.0	8.0	8.5	8.5	8.5
Aug.	7.5	7.5	7.5	8.0	7.5	7.5	7.5
Sept.	7.5	7.5	7.5	8.0	7.5	7.5	8.0
(Oct.	8.0	8.0	8.0	8.0	8.0	8.5	8.5 *)
Alkalinity ppm (Methyl Orange)							
April	-	175	160	185	210	205	210
May	165	175	150	177	199	194	207
June	190	195	180	185	189	190	195
July	200	190	175	200	244	210	210
Aug.	190	160	165	166	180	185	215
Sept.	190	180	160	190	190	190	190
(Oct.	200	240	220	220	210	210	210 *)

* Only one reading

Other figures are average of weekly readings

Table 3 (cont.)

	Athabasca River			Pembina R.	Creeks		
	Hin-ton	Chis-holm	Atha-basca	Flatbush	Irish	French	Chis-holm
<u>CO_2</u>							
April	-	13	14.5	11	3.5	3	3
May	12	11	13	10	3.5	3	3
June	3	3	3	15	3.5	3	3
July	3	3	3	3	3	3	3
Aug.	8	11	11	3	12	13	12
Sept.	9	12	12	3	12	13	14
(Oct.	3	3	3	3	3	3	3 *)
<u>Dissolved Oxygen</u> ppm.							
April	-	8.4	8.5	8.5	8.7	8.9	8.9
May	8.4	8.1	8.4	8.7	8.8	8.9	8.7
June	8.9	8.5	8.4	8.9	8.7	8.5	8.9
July	9.8	9.8	9.5	9.8	8.9	9.4	9.2
Aug.	9.7	9.6	9.5	9.5	9.4	9.8	9.4
Sept.	9.4	9.2	9.4	9.6	9.8	9.8	10.0
Oct.	9.5	9.2	9.0	9.6	9.9	9.9	10.0

HINTON

Hinton (elevation 3265 feet) is about 177 miles west of Edmonton. It lies on the bank of the Athabasca river which has many riffles in which S. arcticum and S. tuberosum breed.

Muskuta creek and three other creeks flowing into the Athabasca river above Hinton were surveyed for black fly species present. S. vittatum, S. venustum and S. arcticum were collected. Adults of Prosimulium travisi and P. onychodactylum were captured in net-sweeps.

ATHABASCA TOWNSHIP AREA

Athabasca town is 40 miles east of Flatbush, situated on the Athabasca river.

In one locality down stream, below the town, and many localities above the town, S. arcticum was collected but in small numbers.

Muskeg creek and three other creeks yielded large samples of black fly larvae, S. venustum being the dominant species.

TAXONOMIC PROCEDURE

The family is very poor in fossil records (Smart 1945 and Stone 1964). The specimens recovered from Oligocene amber (English Purbeck) were described by Westwood (1854) and Handlirsch (1906). Two species belonging to two genera have been named: Simulidium priscum Westwood 1854 orthotype of Simulidium Westwood 1854 and Simulium humidum Brodie 1906 orthotype of Pseudosimulium Handlirsch 1906.

Black flies are distinct and well separated from the other nematocerous families yet they share the biting habit with the Ceratopogonidae. There are no species in the simuliids with affinities to the latter, nor to the chironomids although Shewell (1958) and Davies (1961) reported on the similarities between the primitive simuliids and chironomids, especially in the larval stages. Grenier and Rageau (1960) suggested that the family, a highly evolved nematocerous family, is a precursor of the Brachycera.

Seven subfamilies have been named by Enderlein (1937): Simuliinae, Prosimuliinae, Hellichiinae, Ectemniinae, Cnesiinae, Stegopterninae, and Nevermanniinae. Other authors accepted 2 or 3:

Edwards 1939, Stone 1964 and Stone and Jamnback 1955; Simuliinae, and Prosimuliinae.

Smart 1945: Simuliinae and Parasimuliinae.

Dumbleton 1963, Grenier and Rageau 1960 and Shewell 1958: Simuliinae, Prosimuliinae and Parasimuliinae.

Rubtzov 1959: Simuliinae and Gymnopaidiinae.

There are 80 generic names and 1300 specific names in the literature. The genera and subgenera accepted in North America are:

Simulium Latreille, 1802

Simulium

Eusimulium

Byssodon

Psilozia (_Neosimulium_)

Hagenomyia

Gnus

Cnephia Enderlein, 1921

Cnephia

Stegopterna

Ectemnia

Prosimulium Roubaud, 1906

Prosimulium

Helodon

Parasimulium Malloch, 1914

Parasimulium

Twinnia Stone and Jamnback, 1955

Gymnopais Stone, 1949.

The family is cosmopolitan; _Simulium_ and _Cnephia_ are the most widespread genera. There are species common to most of the adjacent zoogeographical regions.

MATERIAL AND METHODS

Aquatic stages and adults were collected from the field and preserved in 95% ethyl alcohol; some of the adults were pinned or mounted by gluing them on paper points. Laboratory rearing methods were also utilized in the taxonomic study, especially in the determination of the number of larval instars.

The eggs of some species were collected easily but other species proved difficult as the eggs are scattered on the river bottom and no efficient method was found for their extraction. It was found that by combining the eggs, larvae and pupal skins with the adult, identification is feasible. The pupae are more diagnostic than any other stage. Dissection of some stages was of value.

The eggs were measured in an attempt to utilize them in the study. It was found that the linear dimensions of eggs of the species studied have an overlapping range. The eggs of the different species proved difficult to identify positively.

On the other hand the larval head capsule and its different structures were repeatedly employed in keying the species. The antenna has four articles and their colour and length are utilized in the study. The cephalic apotome (frontoclypeus) has head spots which occur where the muscles attach to the dorsal surface of the head capsule. These spots are constant in: anterior and posterior median and anterior and posterior lateral groups. The ventral side of the head capsule has a

number of structures widely used in identification of the species. The shape and size of the postgenal cleft (throat, occipital, epicranial) vary from a slight groove extending to less than one-fifth the distance between the occipital pits and the base of the submental teeth, to a large bulbous opening with an apex almost touching the base of the hypostomial teeth. The submentum (hypostomium, mentum) has three sets of teeth: median tooth, lateral teeth (2 or 3) and a single corner tooth on each side of the laterals. The cephalic fans (head fans or brushes) have short stalks (stems) and the number of rays in the mature larva is fairly constant (usually increases with each instar). Under each primary fan there is a secondary fan. The labrum, mandibles and maxillae are present. The hypopharynx is of no taxonomic value.

The larval proleg has a circlet of hooks at its apex used for locomotion. The lateral sclerite (plate) of the proleg is of subsidiary importance in identification of the species as it varies little from one species to another. The pupal respiratory organ histoblast is of considerable value.

The abdominal features utilized in the study are scales or setae, colouration, ventral papillae (anal tubercles), anal sclerite (anal cross-piece) and the posterior sucker (posterior circlet of hooks).

The pupa is usually surrounded by a cocoon, the shape of which is characteristic. The pupal respiratory organ consists of two to forty filaments arising from a different number of stalks (trunks, petioles).

The filaments may be grouped or not. The hooks on the abdominal segments and the terminal spines are specific. The pupa proved to be a reliable tool of the utmost taxonomic value.

The adult black fly is very difficult to identify. The antennal flagellum has 7-9 articles. The maxillary palpus contains a sensory organ in its third segment. The comparative length of vein R (stem vein, proximal to the common base of R and Rs) and the distance to wing apex from the base of Rs are widely used. The basal cell may be present in some species. The presence of setae or hairs on the ventral and dorsal sides of the veins is a good character for keying some species. The first tarsal articles of the hind leg (the basitarsus) is extended posteriorly in a flattened lobe (calcipala) and the second article is notched dorsally (pedisulcus). The tarsal claws are simple or toothed (forked, bifid).

The sexes are dimorphic and the males are holoptic; the upper facets of the eye in the males are larger than the lower ones. The male genitalia consist of dark pigmented sclerites that can be used to separate the species groups. On each side of the tip of the abdomen lies dorsally the basistyle (coxite, basimere) and attached to it is the clasper (dististyle, distimere) which has a single or many teeth on the inner side. Between the basistyle and clasper is found a ventral plate, a median sclerite and a paramere consisting of two arms and a fringe of hooks (phallosome and aedeagus pile respectively). The female genitalia

consist of an ovipositor lobe attached to sternite eight, a genital fork under tergite nine, an anal lobe and a cercus.

KEYS TO THE GENERA OF NORTH AMERICAN SIMULIIDAE

Adults

1. Costa with fine hairs only (microtrichia) no spiniform setae (macrotrichia); Rs forked apically; no calcipala or pedisulcus 2

   Costa with macrotrichia intermixed with microtrichia; Rs not forked at apex; or with a small fork at the extreme portion; calcipala and pedisulcus present 5

2. A slight or well developed bulla behind the eye; antennal flagellum with 7-9 articles 3

   No bulla behind the eye; antennal flagellum with 9-11 articles . . . . <u>Prosimulium</u> Roubaud

3. R joins the costa near the middle of wing; submedian fold apparently not branched; Rs fork distinctly ending before the termination of costa at apex of wing; flagellum with 9 articles . . . <u>Parasimulium</u> Malloch

   R joining costa well beyond middle of wing; submedian fold forked; Rs fork reaching to or beyond termination of costa 4

4. Scutum with stout, erect hairs but no fine recumbent hairs; flagellum with 7-9 articles . . . . <u>Gymnopais</u> Stone

Scutum with fine recumbent hairs only; 7-9 articles; male clasper with one apical spine; female ovipositor short, not reaching the anal lobes . . . . <u>Twinnia</u> Stone

5. Basal cell usually present; pedisulcus absent or very small; length of R more than one-third the distance from base of Rs to the wing apex, with hairs dorsally . . . . <u>Cnephia</u> Enderlein

Basal cell absent or very small and incomplete; pedisulcus well developed; R with or without hairs dorsally; its length less than one-third the distance from base of Rs to wing apex . . . . . <u>Simulium</u> Latrielle

<u>Pupae</u>

The pupa of <u>Parasimulium</u> has not been described.

1. Cocoon irregular, shapeless and reduced; abdomen with a pair of large terminal spines 2

Cocoon well developed with definite anterior opening; abdomen without terminal hooks 6

2. Almost no cocoon; dorsum without hooks; abdomen with ten hooks on sternites four to six in more than one transverse row; respiratory filaments 2 - 4 (subarctic genus) . . . . . <u>Gymnopais</u>

Cocoon covering part of the body; dorsum with hooks on some of the tergites; if present hooks on the sternites are in a single transverse row . . . 3

3. Tergites 6-8 with anterior row of hooklets 4

Tergites 6-8 without row of hooklets: a) Pupa 4.0 mm long; respiratory organ with three stout trunks branching in 16 filaments . . . . <u>Twinnia</u>

b) Pupa 2.0-3.0 mm long; respiratory organ with two trunks branching in 15-23 (average 19) pale slender filaments . . . . <u>Cnephia</u> <u>abdita</u> Peterson

4. Respiratory filaments arising from a rounded knob on a short petiole . . . . <u>Cnephia</u>

Respiratory filaments not arising from a rounded knob on a short petiole 5

5. Respiratory filaments 12 (rarely 14) or less arising from two trunks . . . . <u>Cnephia</u>

Respiratory filaments more than 12, if less than 12 not arising from two trunks . . . . . . <u>Prosimulium</u>

6. Cocoon stalked and anterior margin not well developed . . . . <u>Cnephia</u>

Cocoon not stalked and anterior margin well developed; lateral margin of terminal segments without short, curved hooks, although setae may be present . . . . <u>Simulium</u>

<u>Larvae</u>

1. Larva without cephalic fans; anal sclerite absent or when present X-shaped 2

Larva with two cephalic fans; anal sclerite Y-shaped or absent 3

2. Labrum normal; antenna extending beyond the short cephalic apotome; mandible with no teeth on the subapical margin; submentum with distinct teeth . . . . <u>Twinnia</u>

Labrum enlarged; antenna not extending beyond the narrow and elongated cephalic apotome; mandible with small teeth on outer subapical margin; submentum with no distinct teeth . . . . <u>Gymnopais</u>

3. Anal sclerite absent . . . . <u>Cnephia</u>

Anal sclerite present 4

4. Antenna with articles one and two pale, three and four darkly pigmented; secondary fan filaments form a straight line at their tips when extended; median tooth of submentum tridentate anal gills with three simple lobes . . . . . Prosimulium

Antenna with articles one and two yellow to brown and three and four rarely dark brown; secondary fan filaments form an arc; median tooth of submentum not tridentate; anal gill with three simple or compound lobes 5

5. Submentum with corner and median teeth large and subequal, lateral teeth three and subequal; a) Ventral papillae absent or very small; postgenal cleft either pointed apically or suboesophageal ganglion and/or epidermis of postgenal cleft distinctly dark, or both; head spots light or dark; anal gill with three compound lobes (except Psilozia and Eusimulium) . . Simulium

b) Ventral papillae well developed; anal gill with three simple lobes (except latipes); postgenal cleft not pointed upwards; suboesophageal ganglion and epidermis of postgenal cleft not black; head spots dark . . . . (Eusimulium)

Submentum not as above; anal lobe with three simple lobes . . . . Cnephia

LIST OF SPECIES OF SIMULIIDAE (DIPTERA) RECORDED FROM ALBERTA

(Publisher's or collector's name and date of publication or collection follow the colon.)

Simulium	(Simulium)	decorum Walker, 1848: Strickland 1938
		hunteri Malloch, 1914: Strickland 1938
		tuberosum Lundstroem, 1911: Fredeen 1958
		luggeri Nicholson and Mickel, 1950: Fredeen 1958
		venustum Say, 1823: Strickland 1938
		verecundum Stone and Jamnback, 1955: Abdelnur 1963
		meridionale Riley, 1886: Fredeen 1958
		malyshevi Dorogostajakij, Rubtzov and Vlasenko, 1935: Fredeen 1958
		piperi Dyar and Shannon, 1927: Fredeen 1958
	(Byssodon)	rugglesi Nicholson and Mickel, 1950: Fredeen 1958
		transiens Rubtzov, 1949: Fredeen 1958
	(Gnus)	arcticum Malloch, 1914: Strickland 1938
		corbis Twinn, 1936: Fredeen 1958
	(Psilopelmia)	griseum Coquillett, 1898: Fredeen 1958
		bivittatum Malloch, 1914: Fredeen 1958

	(Psilozia)	vittatum Zetterstedt, 1838: Strickland 1938
	(Eusimulium)	aureum Fries, 1824: Fredeen 1958
		latipes (Meigen), 1804: Fredeen 1958
		pugetense Dyar and Shannon, 1927: Fredeen 1958
	(Hagenomia)	pictipes Hagen, 1880: Strickland 1938
Cnephia	(Cnephia)	dacotensis Dyar and Shannon, 1927: Abdelnur, 1965
		emergens Stone, 1952: Abdelnur, 1965
		saskatchewana Shewell and Fredeen, 1958: Shewell and Fredeen 1958
Cnephia	(Stegopterna)	mutata (Malloch), 1914: Abdelnur, 1965
	(Cnetha)	saileri Stone, 1952: Fredeen 1958
Prosimulium	(Prosimulium)	fulvum (Coquillett), 1902 : Strickland 1938
		pleurale Malloch, 1914: Strickland 1938
		travisi Stone, 1952: Abdelnur, 1965
		decemarticulatum (Twinn), 1936: Abdelnur, 1965
		onychodactylum Dyar and Shannon, 1927: Abdelnur 1965

Twinnia biclavata Stone and Jamnback, 1955: D.M. Wood 1964

KEYS TO THE SPECIES

PROSIMULIUM

Adult females

1. Antenna with 11 articles 2

   Antenna with 9 or 10 articles . . . . decemarticulatum

2. Claw with a strong thumb-like basal projection 3

   Claw simple 4

3. Integument yellow or orange, frons narrow, nearly parallel sided . . . . onychodactylum

   Integument black, frons normal . . . . pleurale

4. Integument yellow to orange . . . . fulvum

   Integument brown or black . . . . travisi

Adult males

1. Antenna with 9 or 10 articles, clasper with one spine apically . . . . decemarticulatum

   Antenna with 11 articles 2

2. Hind femora at least, yellow 3

   Hind femora brown or blackish, antennae black, ventral plate apically with sharp lateral prongs between which lies a two-tined fork . . . . pleurale

3. Integument of thorax orange, clasper with a single apical spine . . . . <u>fulvum</u>

   Integument of thorax dark or brown-black 4

4. Apex of clasper pointed with two terminal spines; ventral plate broad, shallow and V-shaped; basal articles of hind tarsus swollen and thus broader than other articles . . . <u>onychodactylum</u>

   Apex of clasper rounded, with two apical spines; ventral plate with a narrow and sharply pointed median recurved lip; tarsal articles not swollen . . . . <u>travisi</u>

<u>Pupae</u>

1. Respiratory organ consisting of two stout divergent trunks on a short petiole, from the former arise 12-20 slender filaments . . . . <u>onychodactylum</u>

   Respiratory organ not as above 2

2. Respiratory filaments 9, arranged in a whorl from a short base . . . . <u>decemarticulatum</u>

   Respiratory filaments 16 or more 3

3. Respiratory filaments 21 or more . . . . <u>pleurale</u>

   Respiratory filaments 14 or 16 4

4. Respiratory filaments closely clumped together; dorsum of head and thorax strongly rugose . . . . <u>travisi</u>

Respiratory filaments 16; not closely clumped together; dorsum of head and thorax not rugose; pupa orange . . . . <u>fulvum</u>

<u>Larvae</u>

1. Submental median tooth distinctly shorter than corner tooth 2

   Submental median tooth distinctly longer than corner tooth 3

2. Submental lateral teeth longer than other teeth; antenna longer than cephalic fan stalk, 45 rays in cephalic fan; nine filaments in respiratory histoblast; anal sclerite subrectangular, lateral plate of proleg very narrow . . . . <u>decemarticulatum</u>

   Submental corner tooth longest; antenna longer than cephalic fan stalk, 54 rays in cephalic fan, 21 or more filaments in respiratory histoblast . . . . <u>pleurale</u>

3. Postgenal cleft simple, antenna reaches tip of cephalic fan stalk 4

   Postgenal cleft biarctate, antenna extending three-fourths length of cephalic fan stalk; respiratory histoblast with many filaments arising from two trunks . . . . <u>onychodactylum</u>

4. Postgenal cleft slight, last lateral tooth on submentum as long as median tooth, head capsule pale, dorsal pattern absent, 17-19 rays in cephalic fan, 16 filaments in respiratory histoblast . . . . <u>fulvum</u>

   Postgenal cleft pronounced, last lateral tooth on submentum shorter than median tooth, head capsule pattern consisting of a median broken line and two lateral spots on each side of it with a broad dark area posteriorly . . . . <u>travisi</u>

<u>CNEPHIA</u>

<u>Adult females</u>

1. Tarsal claws simple 2

   Tarsal claws each with a distinct basal tooth or a large projection 3

2. Maxilla with retrorse teeth, mandible serrate, calcipala large, broad, rounded . . . . <u>mutata</u>

   Maxilla without teeth, mandible not serrate, calcipala short, pointed . . . . <u>emergens</u>

3. Tarsal claws with distinct teeth basally, calcipala small, pedisulcus indistinct or

absent, scutum brownish with three narrow pale lines . . . . <u>dacotensis</u>

Tarsal claws with large basal projections 4

4. Scutum with three pale gray vittae, median narrow and straight, lateral broader and sinuous; scutellum with long, erect, white and few black hairs . . . . <u>saskatchewana</u>

Scutum gray, clothed with yellow recumbent hairs, scutellum reddish brown with long, erect pale hairs . . . . <u>saileri</u>

<u>Adult males</u>

1. Clasper with one apical tooth 3

Clasper with two teeth 2

2. Galea of maxilla reduced, shorter than labrum-epipharynx . . . .<u>emergens</u>

Galea of maxilla normal, as long as labrum-epipharynx . . . . <u>mutata</u>

3. Upper facets not distinctly enlarged . . . . <u>dacotensis</u>

Upper facets distinctly enlarged 4

4. Clasper apical tooth very small, basistyle large irregular with an inner apodeme . . . . . . <u>saskatchewana</u>

Clasper apical tooth well developed, basistyle stout, subquadrate . . . . <u>saileri</u>

Pupae

1. Respiratory filaments 12, arising from two main trunks (dorsal 7, ventral 5) . . . . mutata

   Respiratory filaments 12 or more arising from more than two trunks 2

2. Respiratory filaments 12 arising from 3 main trunks; dorsal with 4, lateral with 3 and ventral with 5 filaments . . . . emergens

   Respiratory filaments more than 12 3

3. Respiratory filaments 17-19 on very short trunks arising from a bulbous base . . . . saskatchewana

   Respiratory filaments more than 30 4

4. Respiratory filaments 30-40 in 6 or 7 main groups arising from a short bulbous base . . dacotensis

   Respiratory filaments 35-45 arising near base, no trunks . . . . saileri

Larvae

1. Postgenal cleft reaching base of submentum . . . 2

   Postgenal cleft not reaching base of submentum 3

2. Postgenal cleft reaches beyond base of submentum, 57 rays in fan, 35-45 filaments in respiratory histoblast, submentum teeth

very small . . . . saileri

Postgenal cleft reaches only the base of the submentum, latter with 13 blunt teeth, 17-19 filaments in respiratory histoblast . . . . . saskatchewana

3. Antenna shorter than the cephalic fan stalk . . . . dacotensis

Antenna long extending well beyond cephalic fan stalk 4

4. Head capsule with distinct brown spots on cephalic apotome and posterior region of gena, entire margin of postgenal cleft narrowly pigmented, submentum teeth heavily sclerotized, distal two articles of antenna darker than basal articles, eye spots normal . . . . mutata

Head capsule with indistinct spots, postgenal cleft with lateral margins heavily pigmented, submentum teeth weakly sclerotized, eye spots reduced . . . . emergens

SIMULIUM

Adult females

1. Vein R with hairs dorsally 2

Vein R without hairs dorsally 4

2. Postnotum with a patch of yellow hairs (recumbent scales); scape and pedicel pale brown; legs bicoloured; tarsal claws bifid . . . . <u>aureum</u>

Postnotum bare; antenna dark; claws bifid . . . 3

3. Legs brown with distal portion of each part dark; basitarsus of foreleg long and slender; seven to eight times as long as wide; arms of genital fork diverging from stem at a point half way of total length of fork . . . . <u>pugetense</u>

Legs uniformly brown; basitarsus of fore-leg short and broad: five to six times as long as wide; arms of genital fork diverging from stem at a point two thirds the total length of fork . . . . <u>latipes</u>

4. Tarsal claw with a small subbasal tooth or a basal projection 5

Tarsal claw simple 6

5. Claw with a strong basal projection: a) Frons and terminal abdominal segments shining; fore coxa yellow . . . . <u>rugglesi transiens</u>

b) Frons and terminal abdominal segments pollinose; fore coxa dark . . . . <u>meridionale</u>

Claw with a small subbasal tooth: a) Scutum without vittae; hairs on stem vein pale . . . . . <u>arcticum</u> <u>corbis</u> <u>malyschevi</u>

b) Scutum with distinct dark vittae: i) pale species, fore coxa yellow, tibia with white pollinose, legs bicolour . . . . <u>hunteri</u>

ii) dark species, fore coxa dark, no white pollinose on tibia . . . . <u>piperi</u>

6. Abdomen with distinct black and light grey pattern; fore coxa dark; precoxal bridge absent; fore tibia with conspicuous broad white patch anteriorly, extending two thirds the length of tibia; vittae on dorsum . . . . . . <u>vittatum</u>

Abdomen without pattern 7

7. Abdomen blackish or brown 8

Abdomen greyish-yellow: a) Yellowish species; scutum with orange stripes (vittae) or mesonotum with seven stripes of contrasting colours; frons and abdominal segments pollinose . . . . <u>bivittatum</u>

b) Yellowish-grey species; no vittae or stripes; frons and terminal abdominal segments pollinose . . . . <u>griseum</u>

8. Frons and terminal abdominal tergites

distinctly pollinose; anal lobe large, subquadrate but narrow dorsally and broadening ventrally, anteroventral margin rounded with a short posteroventral projection under cercus: a) Fore tibia with a very distinct patch of white pollen . . . . . <u>decorum</u>

b) Fore tibia with no distinct patch of white pollen . . . . <u>pictipes</u>

Frons and terminal abdominal tergites shining black; anal lobe not as above 9

9. Fore tibia with a narrow greyish-white streak on anterior surface covering not more than one-third the width of tibia; small dark species . . <u>tuberosum</u>

Fore tibia with a bright yellowish-white patch on anterior surface covering more than one-half the width of tibia 10

10. Subcosta without a row of hairs on ventral surface . . . . <u>luggeri</u>

Subcosta with a row of hairs ventrally 11

11. Inner margin of ovipositor lobe straight anterior margin of lobe not more sclerotized than rest of lobe . . . . <u>venustum</u>

Inner margin of lobe concave (with an oval space between the two lobes); anterior

margin of lobe distinctly more sclerotized than

rest of lobe . . . . verecundum

Adult males

1. R with hairs dorsally 2

R without hairs dorsally 4

2. Postscutum with a patch of appressed yellow hair; legs bicoloured; ventral plate with a laterally compressed median keel . . . . aureum

Postscutum bare; legs uniformly brown; ventral plate with no median keel 3

3. Ventral plate broad with a medial V-shaped depression . . . . pugetense

Ventral plate broad but with no depression . . . . latipes

4. Clasper with 3 or more apical spines . . . . vittatum

Clasper with 2, 1 or no apical spines 5

5. Clasper with a stout spine or tubercle at base internally 6

Clasper without spine or tubercle at base 8

6. Base of clasper with a stout spine internally . . . hunteri piperi

Base of clasper with a distinct rounded tubercle internally 7

7. Basistyle with a number of short stout spines . . . .tuberosum

Basistyle with hairs only . . . . rugglesi transiens

8. Ventral plate compressed, with denticles on margins 9

Ventral plate broadly rounded, without denticles on margins . . . . meridionale pictipes

9. Ventral plate narrow (compressed), an inverted Y, with a ventral process or keel 10

Ventral plate broad, without a ventral process or keel: a) Toothed (serrated) margins of ventral plate pointing outwards, visible in profile .venustum

b) Toothed margins folded inwards, not visible in profile or dorsally . . . . verecundum

10. Ventral keel of ventral plate setose, forming an angle before apex of median portion of plate . . . . decorum

Ventral keel of ventral plate concave in profile, the angle it forms being at apex of plate 11

11. Clasper shorter than basistyle, former flat, quadrate 12

Clasper longer than basistyle, cylindrical 13

12. Thorax grey with greenish tinge, median area of scutum not orange . . . . <u>griseum</u>

Thorax dark brown to black, with two anterior pollinose spots . . . . <u>bivittatum</u>

13. Basal arms of ventral plate each with a prong but parameral hooks are small . . . . <u>malyschevi</u> <u>luggeri</u>

Basal arms of plate without prongs, some parameral hooks large 14

14. Parameral hooks consist of distinct small hooks and much larger ones, intermingled . . . . <u>arcticum</u>

Parameral hooks gradually lengthening towards centre . . . . <u>corbis</u>

<u>Pupae</u>

1. Respiratory filaments 4 2

Respiratory filaments more than 4 4

2. Anterior margin of cocoon with a long median projection anteriorly . . . . <u>latipes</u>

Anterior margin of cocoon without a projection 3

3. Dorsal respiratory filament strongly diverging from other three . . . . <u>aureum</u>

Dorsal respiratory filament not divergent:

a) Respiratory filaments paired, distinctly petiolated . . . . <u>pugetense</u>

b) Petioles very short . . . . <u>transiens</u>

4. Six respiratory filaments . . . . <u>tuberosum</u>
<u>verecundum</u>
<u>venustum</u>

Respiratory filaments more than 6 5

5. Respiratory filaments 8: a) In 4 petiolated pairs . . . . <u>rugglesi</u>

b) In 3 petiolate groups: 2 plus 1, 2 plus 1, and 2, dorsal, median and ventral, respectively; cocoon with slightly thickened narrow collar . . . . <u>griseum</u>

c) As above but anterior margin of cocoon broad and distinctly thickened . . . . <u>bivittatum</u>

d) Filaments in 3 petiolated pairs plus 2 single filaments . . . . <u>decorum</u>

Respiratory filaments 9 or more 6

6. Respiratory filaments 9, diverging in a semicircle from centre; cocoon boot-shaped . . . . <u>pictipes</u>

Respiratory filaments 10 or more 7

7. Respiratory filaments 10: a) Cocoon boot-shaped . . . . corbis

b) Cocoon with an anterior projection . . . . piperi

Respiratory filaments 12 or more 8

8. Respiratory filaments 12: a) Cocoon with broad collar (boot-shaped), with many openings anteriorly . . . . arcticum

b) Cocoon with a narrow collar and one large anterior opening . . . . luggeri

Respiratory filaments 14 or more 10

10. Respiratory filaments 14 or 16; cocoon slipper-shaped . . . . vittatum

Respiratory filaments 16; cocoon boot-shaped . . . . malyschevi

Respiratory filaments more than 16 11

11. Respiratory filaments 22-26 . . . . meridionale

Respiratory filaments 100 or more. . . . . hunteri

Larvae

1. Anal gill with three simple lobes 2

Anal gill with three compound lobes 4

2. Ventral papillae conspicuous, conical; head spots dark; suboesophageal ganglion

and epidermis in postgenal cleft pale;
respiratory filaments in histoblast 4: a)
Antenna dark and conspicuous; submentum
darker than adjacent area; lateral head
spots double; anal gill lobes with secondary
bumps . . . . <u>pugetense</u>

b) Antenna pale; posterior half of submentum
concolorous with adjacent area; dorsal head
pattern consisting of longitudinal patches . . . . <u>aureum</u>

Ventral papillae small or absent; sub-
oesophageal ganglion and/or epidermis in
postgenal cleft usually black; respiratory
filaments in histoblast variable 3

3. Submentum with median tooth as long as
corner teeth; second antennal article with
a single lobed ventral pale spot; anal gill
with no accessory lobes; postgenal cleft
slight and rounded apically . . . . <u>vittatum</u>

Submentum with median tooth longer than
corner teeth; second antennal article with
a bilobed ventral spot; anal gill with numerous
accessory lobes; postgenal cleft extending to
more than half the distance to the base of
submentum . . . . <u>pictipes</u>

4. Pigmented area anteroventral to eye conspicuous, suboesophageal ganglion and epidermis in postgenal cleft pale, second antennal article more than twice as long as third, respiratory histoblast with 4 filaments . . . . <u>latipes</u>

   No pigmented area anteroventral to eye 5

5. Suboesophageal ganglion and epidermis in postgenal cleft pale . . . . <u>piperi</u>

   Suboesophageal ganglion and/or epidermis in postgenal cleft dark 6

6. Spots on cephalic apotome (head spots) dark; antenna shorter than cephalic fan stalk; abdomen pale yellowish-brown; respiratory histoblast with 12 filaments; postgenal cleft bulbous extending one half the distance to base of submentum . . . . <u>luggeri</u>

   Head spots pale 7

7. Antenna longer than the cephalic fan stalk: the entire two distal articles extending beyond apex of stalk of cephalic fan: a) Respiratory histoblast with 6 filaments; postgenal cleft uniformly tapering; 43 rays

in cephalic fan . . . . <u>tuberosum</u>

b) Respiratory histoblast with 10 filaments; dorsal head pattern lacking isolated spots; postgenal cleft extending to just below the base of submentum . . . . <u>corbis</u>

c) Respiratory histoblast with 12 filaments; submentum teeth equal in length; 50 rays in cephalic fan . . . . <u>arcticum</u>

d) Respiratory histoblast with 16 filaments; postgenal cleft extends to base of submentum; latter with a distinct long median tooth; 49 rays in cephalic fan . . . . <u>malyschevi</u>

Antenna shorter than cephalic fan stalk 8

8. Ventral papillae conspicuous . . . . <u>rugglesi</u> <u>transiens</u>

Ventral papillae absent 9

9. Postgenal cleft extending to less than half the distance to base of submentum . . . . <u>hunteri</u>

Postgenal cleft extending to more than two thirds the distance to base of submentum 10

10. Infuscation around head spots wide and extending beyond outer edge of antero-lateral spots; arms of anal sclerite broadly fused medially 11

Infuscation around head spots narrow, not extending beyond inner edge of anterolateral spots; arms of genital sclerite narrowly fused medially; respiratory histoblast with 8 filaments . . . . <u>decorum</u>
<u>griseum</u>
<u>bivittatum</u>

11. Lateral plates of proleg lightly sclerotized; cephalic fan with about 52 rays; anal hooks in 66 rows; postgenal cleft not bordered by a fulvous area . . . . <u>verecundum</u>

Lateral plates of proleg heavily sclerotized; cephalic fan with less than 42 rays; anal hooks in about 70 rows; postgenal cleft bordered by a narrow fulvous band . . . . <u>venustum</u>

DESCRIPTIONS OF GENERA AND SPECIES

The descriptions and distribution of genera and species were adapted from the following works: Cameron 1922, Davies *et al.* 1962, Davies 1965, Fredeen 1958, Hearle 1932, Lugger 1898, Malloch 1914, Nicholson and Mickel 1950, Peterson 1960, Rubtzov 1959, Shewell 1958, Shewell and Fredeen 1958, Smart 1944, Sommerman 1953, Stains and Knowlton 1943, Stone 1952, 1963 and 1964, Stone and Jamnback 1955, Strickland 1938 and 1946, Twinn 1936, and Wood *et al.* 1963.

Genus *PROSIMULIUM* Roubaud

Simulium subgenus *Prosimulium* Roubaud, 1906 : Compt. Rend. Acad. Sci. Paris 143 : 521

Type species : *Simulium hirtipes* Fries (designated by Malloch, 1914)

The absence of macrotrichia from the costa and the distinct forking of Rs separate the adult *Prosimulium* from *Simulium* and *Cnephia* (except *Cnephia abdita*); a few superficial characters separate adult *Prosimulium* from *Twinnia* and *Gymnopais*, via generic keys.

There are species complexes, as in other genera, e.g. *P. hirtipes* consists of at least three sympatric species (Davies and Syme 1958). The distribution of the genus follows the line separating the Palaearctic and Nearctic from the Ethopian, Oriental and Neotropical regions. There are common species in the Holarctic (Dumbleton 1963 and Rubtzov 1959).

Prosimulium decemarticulatum Twinn, 1936

Can. J. Res. D. 14 : 110-112, fig. 1d, 1-3 (female, male and pupa).

Holotype : female, type no. 4122 Canad. National Collection.

Distribution: Alaska, Manitoba, New Hampshire, Ontario, Connecticut, Wisconsin, Yukon Territory and Alberta.

A small species; antennae of uniform colour; legs yellow in both sexes; tarsal claws of female deeply bifid; male with a broad ventral plate; wing length 2.6-3 mm; body length 2 mm.

Pupa: 4 mm long; respiratory organ with 9 filaments in a whorl, bent almost at a right angle at origin from a short trunk.

Larva: either whitish to brown or yellow to brown, with regular white intersegmental bands; antenna longer than the stalk of cephalic fan; latter with about 45 rays. Lateral plate of proleg a very narrow, lightly sclerotized horizontal bar. Anal ring with 62-75 rows, 6-7 hooks each. Mature larva 6.5-7.5 mm long.

Prosimulium onychodactylum Dyar & Shannon, 1927

Proc. U.S. National Museum : 69(10), 14 (female)

Holotype: Female, cat. no. 28324, U.S. Nat. Mus.

Distribution: Utah, Oregon, Alaska, British Columbia, California, Colorado, New Hampshire, Wyoming, Ontario, Yukon Territory, and Alberta.

Male considerably darker than the female; tergites and sternites

in both sexes well developed and dark brown. The scutum in the female orange; male basistyle short and stout the clasper short, tapering with two apical teeth; male ventral plate broad.

Pupa: 4.5 - 5.0 mm long, respiratory organ consists of two stout, shallowly ringed clubs arising from a small slender base, dorsal club with 16 slender filaments and ventral club with more than 20 filaments; terminal hooks of abdomen well developed.

Larva: 9.0 mm long, 24 - 28 rays in cephalic fan, secondary projections of the median tooth of submentum basal to the lateral teeth of submentum.

Prosimulium travisi Stone

Prosimulium (Prosimulium) travisi Stone, 1952

Proc. ent. Soc. Wash. 54(2) : 76-77 (female, male and pupa).

Holotype: female, cat. no. 61188, U.S. National Mus.

Distribution: Utah, Alaska, British Columbia, California, Colorado, Yukon Territory, and Alberta.

Female 3 mm long, antennal scape and pedicel yellow; scutum and scutellum with dense yellow hair, erect in latter. Wing 4 mm long; hair on the veins yellow; sternites (2 - 6) undeveloped, ovipositor lobe short, not reaching the apex of cercus.

Male 3 mm long, abdominal sternites well sclerotized, ventral plate transverse with its ventral triangular lip distinct; clasper with two teeth.

Pupa: 5 mm long, respiratory organ with 3 main trunks giving rise to

14 - 16 filaments; abdominal tergites 3, 4 and 8 with stout hooks on their posterior margins; terminal hooks well developed.

Larvae: 7.5 mm long, with 26 rays in the cephalic fan; antenna extending to the tip of cephalic fan stalk.

Genus CNEPHIA Enderlein

Cnephia Enderlein, 1921, Deutsch, tierartzl. Wochenschr. 16 : 199.

Type species: Simulium pecuarum Riley, 1887 (original designation).

Cnephia abdita Peterson is the only species in the genus that lacks macrotrichia on the costa (a Prosimulium character). Some species resemble Prosimulium in minor characteristics and other species are close to Simulium subgenus Eusimulium. This was interpreted as an indication of a polyphyletic origin (Shewell 1958, Dumbleton 1963, Rubtzov 1959 and Stone 1964).

Cnephia is predominant in the Northern Hemisphere. In the Southern Hemisphere 4 species were collected from Chile, 8 from South Africa, 1 from Crozet Island and 6 from Australia. These species show such strong Prosimulium affinities that Rubtzov erected a new genus Paracnephia in 1962 and Davies erected Crozetia in 1965 to contain them.

Cnephia (Cnephia) dacotensis (Dyar & Shannon)

Cnephia dacotensis Dyar & Shannon, 1927

Proc. U.S. National Museum 69(10) : 20 (female, male)

Cotypes: 2 males, cat. no. 28334, U.S. National Mus.

Synonyms: *Simulium* (*Eusimulium*) *lascivum* Twinn, 1936

Eusimulium lascivum (Twinn) : Krafchick, 1943 (mouth parts)

Cnephia lascivum (Twinn) : Davies,1949

Cnephia dacotensis (Dyar & Shannon) : Nicholson & Mickel, 1950

Cnephia (*Cnephia*) *dacotensis* (Dyar & Shannon) : Stone & Jamnback, 1955

Distribution: South Dakota, Iowa, north to Ontario, Rhode Island and Pennsylvania (Transition and Upper Austral zones); also Hudsonian zone at Churchill.

(Recorded from: South Dakota, Iowa, Minnesota, Michigan, Pennsylvania, New York, Massachusetts, Wisconsin, Connecticut, Rhode Island, Saskatchewan, Manitoba, Ontario, Newfoundland, Labrador, and Alberta)

Female: Wing length 2.8 - 3.3 mm; brownish black; antenna black with scape and pedicel reddish; Rs and subcosta with dense hair ventrally; calcipala small, pedisulcus very shallow; claw with a basal swelling and a small tooth; tergites narrow and projecting roof-like over the genitalia; sternites weakly sclerotized.

Male: Sternites 3 - 7 large and well sclerotized; clasper with one tooth; basistyle and clasper large.

Pupa: 4 - 6 mm long; respiratory organ with 6 or 7 trunks, 30 -

40 filaments which branch further near their tips, the respiratory organ base a peculiar swollen knob-like structure; tergites 6 - 8 each with an anterior row of spines; terminal hooks very strong.

Larva: 11 mm long; head capsule with distinct brown spots surrounded by a dark fulvous area; submentum with a large median tooth, 6 small lateral teeth and moderate corner teeth; cephalic fan with 41 - 49 rays, ventral tubercles absent; anal hooks 11 - 17 in about 61 rows.

Cnephia emergens Stone

Cnephia emergens Stone, 1952

Proc. ent. Soc. Wash. 54 : 80 - 81 (female, male)

Holotype: Female cat. no. 61189, U.S. National Mus.

Distribution: Alaska, Ontario and Alberta.

Female: 2.0 - 2.5 mm long, antenna yellow brown, 11 articles; scutum dark brown, clothed with yellow recumbent hairs; hairs on base of costa, stem vein and R_1 dark brown; legs yellow brown calcipala well developed, pedisulcus absent.

Male: Scutum deep brown black with dark yellow brown hairs; abdomen yellow brown; anterior tergites well sclerotized; posterior tergites and the sternites weakly sclerotized; basistyle subquadrate, clasper with a single stout spine at the apex, inwardly bent; ventral plate subquadrate.

Pupa: Respiratory organ consists of three main trunks giving rise

to four dorsal, three lateral and five ventral slender filaments; cocoon irregular, shapeless and stalked.

Larva: 5.5 mm long; antenna longer than the cephalic fan stalk; 50 rays in cephalic fan; submentum median tooth long and slender.

Cnephia mutata (Malloch)

Prosimulium mutatum Malloch, 1914

U.S. Dept. Agric., Bur. Ent., Tech. Ser. 26 : 20 - 21, plate 2, fig. 18 (female).

Holotype: Female cat. no. 15404, U.S. National Mus.

Synonyms: Eusimulium mutatum (Malloch) : Dyar & Shannon, 1927

Eusimulium mutatum permutatum Dyar & Shannon, 1927

Mallochella mutatum (Malloch) : Enderlein, 1930

Simulium (Eusimulium) mutatum (Malloch) : Twinn, 1936

Cnephia mutatum (Malloch) : Davies,1949

Distribution: Canadian, Transition and Upper Austral zones from Alaska and Labrador to California, Wyoming, Arkansas and Alabama.

Female: Wing length 3.5 mm; grayish black; frons and clypeus with yellowish hairs; vesicle of sensory organ in third segment of maxillary palpus about one-third the length of segment; scutum dark brownish gray with pale yellow recumbent hairs; calcipala extending one-third length of second tarsal segment, no distinct pedisulcus; claws simple; abdomen brown, sternites not sclerotized, anal lobe narrow and extends under cercus.

Male: Darker than female; scutum may show stripes at certain light reflections; sternites large and sclerotized; clasper with a pair of teeth apically; ventral plate broad; median sclerite Y-shaped.

Pupa: 3 - 4 mm long; respiratory filaments 12 arranged in an upper trunk with 4 plus 3 filaments and a lower trunk with 3 plus 2 filaments; terminal hooks well developed, cocoon poorly developed.

Larva: 6 mm long; head capsule with no dark fulvous area around head spots but a yellow isthmus separating the five anterior and four posterior median head spots, one lateral spot on each side posteriorly; submentum with a median tooth, two small lateral teeth, a large broad lateral tooth with a small tooth on inner and two projections (teeth-like) in outer slopes; cephalic fan with about 54 rays; anal hooks 11 - 13 in 60 rows; anal sclerites well sclerotized.

Genus SIMULIUM Latreille

Simulium Latreille, 1802

Hist. Nat. Gen. part Crust. Inst. 3 : 426.

Type species: Rhagio colombaschensis Fabricius, 1787 (by original designation of Latreille)

Synonyms: Discosphyria Enderlein, 1922

Gynonychodon Enderlein, 1925

Simulium (Pseudosimulium) Baranov, 1926

Psaroniocompsa Enderlein, 1934

Aspathia Enderlein, 1935

Simulium (_Danubiosimulium_) Baranov, 1935

Psilocnetha Enderlein, 1935

Simulium (_Cleistosimulium_) Seguy & Dorier, 1936

Pliodasina Enderlein, 1936

Pselaphochir Enderlein, 1936

All Simuliids were known as _Simulium_ up to the time of the start of the family classification except for the two fossil genera (page 16).

The following Nearctic subgenera are fairly well accepted:

Eusimulium Roubaud, 1906

Simulium Latreille, 1802

Psilozia Enderlein, 1937

Gnus Rubtzov, 1940

Hagenomyia Shewell, 1959

Boophthora Enderlein, 1921

Byssodon Enderlein, 1925

Hearle Vagas, Martinez Palacios & Diaz Najera, 1946

Hemicnetha Enderlein, 1935

Psilopelmia Enderlein, 1937

Simulium (_Gnus_) _arcticum_ Malloch

Simulium arcticum Malloch, 1914

U.S. Dept. Agr. Bull. ent. Tech. Ser. 26 : 37, fig. 4 (female).

Holotype: Female cat. no. 15410, U.S. National Mus.

Synonyms: *Simulium simile* Malloch (apud Dyar & Shannon, 1927)

Simulium brevicerum Knowlton & Rowe (apud Stains & Knowlton, 1943)

Simulium nigresceum Knowlton & Rowe (apud Stains & Knowlton, 1943)

Simulium corbis Twinn (apud Stains & Knowlton, 1943)

Distribution: Alaska, Alberta, Saskatchewan, British Columbia, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Washington, Wyoming, Utah, and Yukon Territory.

Description: Cameron (1918, 1922) and Curtis (1954)

Simulium (*Eusimulium*) *aureum* Fries

Eusimulium aureum Fries, 1824

Observationes Entomologicae 1 : 16 (male, female)

Paratypes: Two females, Zoological Institute, Univ. of Lund, Lund, Sweden.

Synonyms: *Melusina aurea* (Fries) : Lundstroem, 1911

Simulium aureum (Fries) : Edwards, 1915, 1920

Puri, 1925

Nicholson & Mickel, 1950

Grenier, 1953

Nevermannia auroa (Fries) : Enderlein, 1921

Cnetha aurora (Fries) : Enderlein, 1922 (misspelling)

Eusimulium aureum (Fries) : Dyar & Shannon, 1927

Heale, 1932

Stains & Knowlton, 1943

Simulium (Eusimulium) aureum Fries : Twinn, 1936

Smart, 1944

Vargas, Martinez & Diaz, 1946

Sommerman, 1953

Simulium bracteatum Coquillett, 1898

Johannsen, 1903

Strickland, 1913

Malloch, 1914

Jobbins-Pomeroy, 1916

Eusimulium aureum bracteatum (Coquillett) : Dyar & Shannon, 1924

Simulium bracteatum (Coquillett) : Johannsen, 1934

Simulium angustipes Edwards, 1915

Friederichs, 1921

Simulium obtusum Dyar & Shannon, 1927

Eusimulium pilosum Knowlton & Rowe, 1934

Simulium (Eusimulium) pilosum Knowlton & Rowe; Twinn, 1938

Eusimulium utahense Knowlton & Rowe, 1934

Simulium (Eusimulium) donovani Vargas, 1943

Simulium diazi De Leon, 1945

Distribution: Holarctic

Nearctic: from Alaska and Maine to Guatemala. Recorded from: Utah, Alaska, Alberta, British Columbia, California, Colorado, Idaho, Nevada, Oregon, Washington, Wyoming, Yukon Territory, Connecticut, Guatemala.

Female: Wing length 2.75 - 3.0 mm; dark grayish, covered with glistening golden yellow fine hairs; scutum, scutellum and postscutellum with recumbent yellow hairs; wing veins yellow brown, hairs on costa and stem vein pale yellow, subcosta with hairs beneath; calcipala and pedisulcus distinct, abdomen dark with yellow to silvery hairs, sternites not sclerotized, claws strongly bifid.

Male: Darker than female, hairs more golden; scutum with golden-yellow hairs, pleural tuft yellow, haltere yellow; abdomen dark with golden-yellow hairs, sternites well sclerotized, clasper short with an apical tooth, paramere with a single hook.

Pupa: 4 mm long, respiratory organ with 4 slender filaments: upper pair with a short petiole, the filaments divergent, lower pair with no petiole and not divergent; terminal abdominal hooks very short; cocoon with a thick rim-like collar.

Larva: 7 mm long, cervical cleft U-shaped, width and length subequal, cephalic fan with 40 - 45 rays; ventral tubercles conspicuous, anal gill with three simple lobes, anal sclerite distinct, darkly pigmented, anal hooks about 11 in 60 - 65 rows.

Simulium (Eusimulium) latipes (Meigen)

Atractocera latipes Meigen, 1804

Klass. u. Beschr. europ. Zweifl. Inst. 96 (male)

Holotype: male (?)

Synonyms: Simulia latipes (Meigen) : Meigen, 1818

Melusina latipes (Meigen) : Lundstroem, 1911

Simulium latipes (Meigen) : Edwards, 1915

Edwards, 1920

Nicholson & Mickel, 1950, Friederichs, 1921

Freeman, 1950, Puri, 1925, Grenier, 1953

Cnetha latipes (Meigen) : Enderlein, 1921

Simulium (Eusimulium) latipes (Meigen) : Twinn, 1936

Sommerman, 1953; Stone & Jamnback, 1955

Distribution: Holarctic and Oriental

Nearctic: Hudsonian and Canadian Zones from Alaska and Maine to California and Connecticut.

Female: 1.5 - 2.5 mm long; wing length 2.5 - 3.0 mm; antenna dark brown to black; scutum with yellow recumbent hairs, scutellum with dense recumbent hairs, postscutellum without recumbent hairs; subcosta with scattered hairs below, stem vein with pale hair; calcipala short and broad, pedisulcus deep; claws with very prominent projections sub-basally; anal lobe subquadrate with a ventroposterior notch, ovipositor short.

Male: Wing length 2.4 - 2.8 mm long; dorsum as in female; abdomen velvety black or reddish brown with dark hair, tergites broad, sternites sclerotized; clasper with a small apical tooth.

Pupa: 2.3 - 3.0 mm long; respiratory organ with four slender filaments arising from a short trunk, the ventral pair with a longer petiole than the dorsal pair; terminal abdomen hooks short and blunt; cocoon with a long tapering median projection and a well developed anterior margin.

Larvae: 6.2 - 6.7 mm long; submentum with a median tooth, three lateral teeth and a corner tooth; cephalic fan with 45 rays; anal gill with three compound lobes, anal hooks 10 in about 85 rows.

Simulium (*Simulium*) *decorum* Walker

Simulium decorum Walker, 1848

List Diptera British Museum : 1 : 112 (female)

Holotype: Female, British Museum, London, England

Synonyms: *Simulium decorum* Walker : Dyar & Shannon, 1927

Stains & Knowlton, 1934, Nicholson & Mickel, 1950

Grenier, 1953

Simulium (*Neosimulium*) *decorum* Walker : Rubtzov, 1940

Simulium (*Simulium*) *decorum* Walker : Sommerman, 1953

Simulium piscicidium Riley, 1870; Osborn, 1896

Malloch, 1914; Johannsen, 1913

Simulium venustum var. *piscicidium* Riley : Johannsen, 1903

Simulium venustoides Hart, 191

Simulium nolleri Friederichs, 1920, Puri, 1925

Smart, 1920

Simulium subornatum Edwards, 1920

Simulium tenuimanus Enderlein, 1921

Simulium decorum katmai Dyar & Shannon, 1927

Hearle, 1932

Simulium (Simulium) ottawaense Twinn, 1936

Distribution: Holarctic

Nearctic: Hudsonian, Canadian, Transition and upper Austral Zones from Alaska and Maine to Iowa and Georgia.

Female: 3.1 - 4.0 mm long; wing length 3 - 3.5 mm long; antenna dark brown, scape, pedicel and first articles orange brown; frons dusted with gray; scutum distinctly convex laterally; subcosta with hairs beneath; fore coxa yellow with white pruinosity; claws simple; sternites one to seven not sclerotized, tergites with a thin gray pollinosity, ovipositor lobe with inner margin sclerotized, genital rod with a very tapering subapical tooth.

Male: Clypeus with gray pruinosity, scutum strongly convex in profile with dense yellow hair wing vein yellowish brown, subcosta with no hairs, sternites 3 to 7 sclerotized, basistyle subquadrate, clasper twice as long as basistyle with a large subapical tooth, ventral plate with a hairy ventral keel.

Pupa: 3.4 - 4.7 mm long; respiratory organ longer than one-third body length, consisting of a dorsal pair 2 ventral pairs on petioles and 2 separate filaments; abdominal terminal hooks very short, cocoon wall vase shaped.

Larva: 8 mm long, separate fulvous areas around the 4 different groups of head spots, cervical cleft bulbous and, pointed apically and extending one-third distance to submentum teeth; cephalic fan with about 50 rays (48 - 53), anal sclerite doubly pigmented, anal hooks 9 - 16 in about 75 rows.

Simulium (Simulium) luggeri Nicholson & Mickel

Simulium jenningsi luggeri Nicholson & Mickel, 1950

Minn. Tech. Bull. 192 : 54. Figs. 71 & 72 (male, female, pupa)

Holotype : Male, Univ. Minn. Collection

Note: Simulium (Simulium) luggeri Nicholson & Mickel : Stone, 1964

This species is very close to S. jenningsi Malloch, both are in the venustum complex.

Female: 1.5 - 2 mm long; wing length 2.0 - 2.5 mm long; antenna dark brown with 11 articles; clypeus quadrate with gray pollinosity; scutum, scutellum and postscutellum glossy dark gray; hairs on stem vein coppery; legs yellow with middle and hind coxae dark; claws simple; anal lobe triangular, cercus triangular; genital rod narrow with divaricate arms, heavily sclerotized distally and with a ventral tooth.

Male: Antenna brown; clypeus dark; scutum velvety black with shiny

marginal spots anteriorly; wings clear; subcosta without hairs; basistyle with a single subapical tooth on inner margin.

Pupa: Respiratory organ with a short basal part branching in 3 trunks with 4, 2 and 2 filaments and 4 separate filaments.

Larva: Head spots not clear; submentum with subequal median and corner teeth and 4 short lateral teeth; the outer slope of submentum (beyond the corner teeth) with 5 heavily sclerotized projections; epidermis and suboesophageal ganglion in cervical cleft colourless; pupal respiratory histoblast with 12 filaments.

Simulium (Simulium) tuberosum (Lundstroem)

Melusina tuberosum Lundstroem, 1911

Acta Soc. Fauna Flora Fenn. 34(12) : 14 (male)

Holotype: Male (?)

Synonyms: Simulium tuberosum (Lundstroem) : Edwards, 1915, 1920 Puri, 1925

Simulium perissum Dyar & Shannon, 1927

Simulium vandalicum Dyar & Shannon, 1927

Simulium (Simulium) perissum Twinn, 1936

Simulium (Simulium) turmale Twinn, 1938

Simulium twinni Stains & Knowlton, 1940

Simulium (Simulium) tuberosum (Lundstroem) : Sommerman, 1953

Distribution: Holarctic

Nearctic: Hudsonian from Alaska to Greenland and south to Upper Austral of Texas and Florida.

Female: Wing length 2.5 - 3.0 mm; frons shiny black and divergent above, clypeus with gray pruinosity; scutum with short yellow recumbent hairs, scutellum brownish black with a margin of erect hairs and a few recumbent yellow hairs; subcosta with hairs below; fore coxa yellowish, middle and hind coxae black, fore tibia flattened with large patch of white hairs, claws simple, sternites 1 to 7 not sclerotized, genital fork with tapering arms, each with a broad blunt tooth.

Male: Wing length 2.4 - 2.7 mm long; scutum velvety black with recumbent hairs, scutellum reddish brown with erect hairs; subcosta bare; sternites sclerotized clasper flattened on distal half with a rounded lobe bearing spicules, apex rounded with a subapical spine arms of ventral plate nearly parallel, numerous hooks on parameral arms.

Pupa: 3 mm long; respiratory organ with three pairs of filaments on short petioles, no terminal hooks, cocoon with strong anterior opening (collar).

Larva: 5.2 - 5.75 mm long; head spots indistinct or absent; cephalic apotome with a dark subtriangular area posteriorly, cervical cleft V-shaped, cephalic fan with 38 - 43 rays, suboesophageal ganglion black abdomen black with broad white intersegmental areas anal sclerite darkly pigmented, anal hooks 11 - 15 in 72 rows.

<u>Simulium</u> (<u>Simulium</u>) <u>venustum</u> Say

<u>Simulium</u> <u>venustum</u> Say, 1823

Jour. Acad. Nat. Sci. Philadelphia 3 : 28 (male, female)

Holotype: Female (lost?)

Synonyms: <u>Simulium</u> <u>molestum</u> Harris, 1841

<u>Simulium</u> <u>minutum</u> Luggeri, 1896

<u>Simulium</u> <u>irritatum</u> Luggeri, 1896

<u>Boophthora</u> <u>rileyana</u> Enderlein, 1922

<u>Simulium</u> <u>groenlandicum</u> Enderlein, 1935

Distribution: Holarctic

Nearctic: Hudsonian from Alaska to Greenland and south to Lower Austral zone of Mississippi and Texas.

Female: Same as <u>tuberosum</u> except for: pleural tuft of hairs usually yellowish, hairs at base of costa and on stem vein yellowish.

Male: Same as <u>tuberosum</u> except for: hairs on scutum white or pale, ventral plate with its central portion trough-like with spines on margin; arms of ventral plate divergent and with no lateral projections.

Pupa: Very similar to <u>tuberosum</u> except the filaments longer and dorsal pair somewhat divergent.

Larva: 6 to 7 mm long; head capsule with distinct yellow head spots; 4 median anterior, 7 to 8 fused medioposterior, 4 mediolateral and 4 fused posteriolateral; distinct dark fulvous areas around the head spots and extend beyond the anterior and posterior groups; narrow isthmuses

separate the anterior and posterior groups of head spots; cervical cleft bulbous, arrowhead-shaped; antenna light yellow cephalic fan with 51 rays; abdomen dirty gray or brown in preserved specimens, anal sclerite darkly pigmented, anal hooks 9 - 15 in 60 - 75 rows.

Simulium (Simulium) verecundum Stone & Jamnback

Simulium (Simulium) verecundum Stone & Jamnback, 1955

New York State Mus. Bull. 349 : 83 (female, male, pupa)

Holotype: Male, no. 62361, U.S. National Mus.

Female: Wing length 2.3 - 3.5 mm; some have the hairs on the stem vein and pleural tuft pale as in venustum and have dark hairs as in tuberosum; the scutum is shinier than in other members of the complex.

Male: Same as venustum except terminal plate with lateral serrated margin of trough turned inwards.

Pupa: Respiratory organ with 6 slender filaments, 2 pairs with very short petioles and very close to each other while the third pair has a longer petiole and divergent.

Larva: Submentum with a distinct large median tooth, 3 lateral teeth and 1 corner tooth; suboesophageal ganglion distinctly dark.

Simulium (Psilozia) vittatum Zetterstedt

Simulia vittata Zetterstedt, 1838

Insecta Lapponica, 1838 - 40 : 803 (female)

Holotype: Female, Zetterstedt Collection at Univ. Lund, Lund, Sweden

Synonyms: Wilhelmia vittata (Zett.) : Enderlein, 1921

Simulium (Simulium) vittatum Zett. : Twinn, 1936

Simulium (Neosimulium) vittatum Zett. : Rubtzov, 1940 Sommerman, 1953; Stone & Jamnback, 1955; Peterson, 1960

Simulium tribulatum Lugger, 1896

Simulium glaucum Coquillett, 1902

Simulium venustoides Hart, 1917

Simulium decorum Walker : Dyar & Shannon, 1927

Psilozia groenlandica Enderlein, 1936

Simulium asakakae Smart, 1944

Distribution: Hudsonian, Canadian, Transition and Upper Austral zones from Alaska and Greenland to southern California and Georgia.

Female: Wing length 3 - 3.5 mm; frons and clypeus gray with white hairs; antenna with scape and pedicel dark reddish and flagellum black with pale pubescence; scutum gray, clothed with short recumbent gray hair; dorsum with black and gray patterns (vittae); pleural tuft white; wing veins yellowish, hairs on stem vein and base of costa white, subcosta bare; calcipala short pedisulcus deep, claws simple; abdomen velvety black or gray with black patterns, which become three stripes posteriorly, sternites 1 to 7 not sclerotized, genital rod with a swollen basal knob, arms divergent each with a narrow ventral lobe and a broad blunt dorsal lobe.

Male: Wing length 2.3 - 3.0 mm; scutum brownish black with a pair

of indistinct grayish stripes, scutellum with erect pale hair, wing veins yellow brown, subcosta bare, legs dark brown; fore tibia with a white patch anteriorly extending to two thirds of the outer margin and one third of inner margin; mid and hind tibiae with the white patch in basal halves, basitarsus with white patch on basal two thirds, in basal third of second tarsus; sternites 3 to 8 sclerotized, basistyle short, clasper two thirds length of basistyle, flattened with 3 to 4 teeth on outer distal margin.

Pupa: 3.0 - 3.5 mm long; respiratory organ with 16 filaments (14 and more rare 15), terminal hooks very short, cocoon wall vase-shaped.

Larva: 9 mm long; head spots dark brown with narrow infuscation around median, anterior and posterior rows; suboesophageal ganglion black; cephalic fan with 50 rays anal sclerite with darkly pigmented arms, anal hooks 18 - 24 in about 67 - 88 rows.

LIFE HISTORIES

Prosimulium (P.) decemarticulatum

This ornithophilic species was collected in 1965 from Irish and Flatbush creeks. The larvae were abundant in May but not before that, indicating that the species passes the winter as eggs. Mature larvae and pupae were taken on June 17. The first adult (a male) emerged in the laboratory on June 24, the females emerged on June 26. In the field a net collection on June 27 yielded only males, later collection yielded both sexes. The females showed no maturation, but were fertilized and most of them had fed on blood. These blood fed females matured their eggs in six days in the laboratory. A few parous females were also collected indicating that the females developed more than one gonotrophic cycle. After July 20 the aquatic stages were encountered singly or in a very random pattern. Similar data were reported by Anderson and Dicke (1960) from Wisconsin, Davies (1950) and Davies et al. (1962) from Ontario, and Sommerman et al. (1955) from Alaska.

Although females did not feed on sparrows in captivity most of the trap collections were from near nests of birds. Females were aspirated from young sparrow chicks in the nests. This is in accordance with the reported host preference for the species (Bennett 1960, Davies and Peterson 1956 and Davies et al. 1962).

Prosimulium (P.) onychodactylum

Three larvae and two pupae of this species were collected in July 1965 and four females and one male were collected on October 2 - 4, 1964. Except for P. travisi this was the rarest species in the study area. Aquatic stages were collected only from the Athabasca river in the Hinton area. Both sexes were attracted to the collector but neither landed nor fed on him. Two dissected females contained well developed ovaries, i.e. the eggs more than half mature.

Sommerman et al. (1955) reported this species to overwinter in the eggs in Alaska and to have one generation annually extending from April to September. Peterson (1959) collected only larvae in Utah and suggested that the species has one generation a year there.

Prosimulium (P.) travisi

On October 4 in the Hinton area a single male of P. travisi was collected in a net sweep from the vegetation on the bank of the Athabasca river, together with six females of S. arcticum. Neither aquatic stages nor females of this species were encountered.

Sommerman et al. (1955) collected P. travisi from July to September. It was suggested that it has one generation a year with the eggs hatching in June.

Cnephia (Stegopterna) mutata

Basrur and Rothfels (1959) discovered that the populations of

C. mutata in southern Ontario contain bisexual diploid forms and parthenogenetic triploid forms (females only). Davies (1950), Davies and Peterson (1956) and Davies et al. (1962) found that 90 - 100% of the individuals collected in Ontario were parthenogenetic females.

Basrur and Rothfels (1959) reported the species as univoltine in Peel county; the eggs of the diploid form hatch in January to February and the triploid form then dominates from mid April to May.

Anderson and Dicke (1960) found that this species passes the winter as eggs in Southern Wisconsin and as larvae in the north.

Davies (1950) collected males and females of the diploid form of the species emerging in mid-May and the peak of emergence of the triploid was in late May extending into June (with an odd female collected in August). This attenuated emergence led Basrur and Rothfels to suggest two generations for this species in southern Ontario.

In the study area larvae of C. mutata were collected after the ice break up. They commenced to pupate on May 14 (1965). The females emerged ten to fifteen days later with their ovaries well developed, containing between 190 - 250 eggs three-fourths mature. These eggs took five to seven days to mature in the laboratory, without fertilization, the females being fed on water and sugar crystals. In the field unfertilized females were collected feeding on horses and to a lesser extent on cows. These females were examined by me and showed indications of a previous ovarian cycle. There were mature eggs in one or both

ovaries intermixed with very immature eggs and plenty of follicular relics.

Fallis (1964) quoted various authors reporting C. mutata feeding on deer, hare, cow and man (ear).

On one occasion an ovipositing female was observed flying low over the surface of water against the current and tapping the water with the tip of its abdomen, it finally fell into the water.

There were no collections of adults or aquatic stages after June 11.

Cnephia (C.) dacotensis

C. dacotensis is univoltine and fully autogenous species. It breeds in Irish creek and was not collected from any other locality. The eggs hatched after the ice break up and the larvae appeared in May and commenced to pupate in May 17 - 20. The first male was collected on May 20 and females two days later. In the laboratory the females raised from pupae showed the eggs almost three-quarters mature. The females fed on water and sugar, matured their eggs in four to six days. In the field females netted from the vegetation on May 24 were all fertilized, their eggs three-fourths mature and the abdomens distended with liquid in the stomach, diverticula and oesophagus. Mating took place on rocks and stones near the water edge,occupying from less than a minute to three minutes. No fertilization plugs or spermatophores were detected.

The females oviposited while flying low over the water. The total number of eggs in their ovaries was 276 to 288. Gravid females netted from the vegetation showed indications of partial oviposition i.e. 20 to 30 ovarioles extended although the eggs were in the same degree of maturation.

The mouth parts of the female were reported as weak, reduced and incapable of feeding (Krafchick 1942, Peterson and Wolfe 1958, Nicholson 1945 and Stone 1964). Twinn (1936), Davies (1950) and Davies and Peterson (1956) compared the size of the male eye with other species and concluded that the eyes are reduced and there is a lack of phototaxis rendering this species incapable of forming a mating swarm. In the present study no feeding or blood engorged females were encountered.

The last date on which the aquatic stages were seen was June 29; although Fredeen (1961 in Davies *et al.* 1962) reported some eggs hatching in autumn.

My findings are in accordance with the reports of Anderson and Dicke (1960), Davies (1950), Davies and Peterson (1956), Davies *et al.* 1962 and Nicholson and Mickel (1950), Sommerman *et al.* 1955, Stone 1964 and Stone and Jamnback 1955.

Cnephia (*C.*) *emergens*

C. emergens was taken as larvae and pupae on May 27 and June 10 respectively from Irish and Flatbush creeks. As no overwintered larvae were detected it is considered to pass the winter in the egg. No

females were taken in the field but laboratory raised females contained half mature eggs. The eggs ranged from 125 - 211 per female. The females fed on water and sugar crystals but not on a sparrow, a cat or my arm. In describing the species Stone (1952) pointed out the reduction in armament of the mandibles and maxillae which indicated inability to feed on blood. The same condition was reported by Davies and Peterson (1956) and Peterson and Wolfe (1958). Davies _et al._ (1962) and Sommerman _et al._ (1955) found a single generation annually, which I confirm.

Simulium (G.) arcticum

This species is the cattle pest of Western Canada. Serious outbreaks have been reported since 1912 in Saskatchewan (Arnason _et al._ 1949, Cameron 1918 and 1922, Curtis 1954, Fredeen 1958 and 1960, Fredeen _et al._ 1951 and 1953, Hearle 1932 and Rempel and Arnason 1947). The life history and control measures were studied in detail by these authors.

On no occasion were the eggs of this species collected from the breeding sites although presumed ovipositing females were captured in several instances from the Athabasca and less frequently the Pembina rivers. Ovipositing females were seen flying over the breeding sites which were mainly rapids and riffles in the rivers. They lay the eggs singly and they do not dive under water to lay (Cameron 1922 and Fredeen 1958 and 1960). The eggs are scattered in the bottom of the river but

my efforts to recover them by brine flotation were not successful. Females captured while ovipositing were kept alive in vials in the laboratory for four days; they did not oviposit and the dissected eggs did not hatch.

Larvae were collected on May 10, 1964 and May 11, 1965. They accumulate in favourable sites within the breeding localities. They attach to pebbles, stones, rocks and vegetation, although the first three are more abundant in these breeding stations than vegetation it was noticed that there was an aggregation of larvae in the different instars on particular substrates i.e. up to the third instar larvae are found on smaller pebbles and stones, later instars on stones and rocks, and mature larvae and pupae on rocks and vegetation in slower flowing water. This indicates a definite migration pattern. Larvae and pupae were collected from the two rivers only although in the southern parts of the province they have been collected from the tributaries of the South Saskatchewan river and from irrigation canals (Fredeen 1958, 1960).

The data indicate that there are four generations per year with an obvious overlapping of successive generations (as indicated by larval density assessment, Fig. 5). The species overwinters in the egg stage as no larvae were collected from under the ice and because the larvae appear after the ice break-up in April. These newly hatched larvae reach maturity at different times in the period from April 20 to May 19

(1964-1965). Pupation of these larvae commences on May 28 and the adult emerges in six to ten days. In the field males were collected two days before the first females were encountered. The overall ratio of females to males was 1 : 4 near the breeding sites and 16 : 1 near grazing cattle and horses; random samples of pupae in the laboratory yielded a 1 : 1 ratio. Average date of pupation for the first complete summer generation is July 1, second generation August 2, the last seasonal generation September 1.

Females emerging from the overwintering eggs have their ovaries well developed indicating an autogenous condition: thus this species fits into Rubtzov's (1963) category of "facultative blood suckers" which includes all the species of blood sucking groups that utilize the larval food reserves for the development of the first batch of eggs. Fredeen (1963) and Fredeen et al. (1951) observed this fact and were able to determine the number of previous ovarian cycles using the criterion of the follicular relics. Females that seek a blood meal have mated, oviposited, and usually have fluid in their crops sweet to taste and giving a positive reaction with Benedict solution. In the present study females feeding on cattle and horses were dissected and the ovaries were noticed to be empty except for a few (1-3) mature eggs and in an expanded condition.

Simulium (S.) aureum

Dunbar (1958, 1959) reported seven cytological forms of this species from larvae collected within its range: the two forms studied were:

Form A: Southern and central Ontario (the only form in Algonquin

Park, Davies _et al._ 1962), with two generations extending from May-October (Davies and Peterson 1956) and females feeding on birds on trees about 20 feet above the ground (Davies _et al._ 1962, Bennet 1960). Form B: Southern Ontario; two or more generations a year.

Jobbins-Pomeroy (1916) reported that _S. aureum_ has five or six generations annually in southern California; two generations were reported from Illinois (Forbes 1912), Britain (Edwards 1920), France (Pacaud 1942), Ontario (Davies 1950, Davies and Peterson 1956), New York (Stone and Jamnback 1955) and Ontario (Davies _et al._ 1962). Stone (1964) reported two or more generations annually from Connecticut; Peterson (1956) reported three or four generations a year in Utah and Sommerman _et al._ (1955) reported one or two generations per annum in Alaska.

This species passes the winter in the egg stage throughout its range. In the study area eggs hatch in late May or early June but adults were first collected in the period June 17 - 19 (1963-1965). The second generation pupated from July 11 to 17 and the third pupated from August 9 to 15. Adult collections indicated three peaks corresponding to the observed increases in the aquatic stages.

Females emerged with their ovaries very small and the eggs not developed (Stage 1 : Christophers' classification 1960). No mating swarms were seen although females collected feeding on cattle and on sticky traps were fertilized. These showed no follicular relics. It may be concluded that _S. aureum_ requires a blood meal for each gonotrophic

cycle. They were not attracted to humans or to other moving objects.

Ovipositing females were observed and sampled from Irish and Flatbush creeks only, which may explain the deficiency in larval contribution to adult nutrients and the slow maturation of the larvae as these are clear streams with only patchy vegetation.

Simulium (S.) decorum

The species is abundant in the area. The overwintering eggs hatch in May and mature larvae and pupae were encountered in 1964 - 65 between May 30 - June 7. These aquatic stages are found as aggregates on undersurfaces of stones, culvert walls, embankments, beaver dams and vegetation leaves. Three more generations were recorded: the pupation commenced in June 16 - 20, third July 22 - 25, and fourth August 11 - 19 (1963 - 65). Apparent overlapping is observed between the first and second generations early in the season and third and fourth generations later in the season. Previous records show the species with two or more generations from Alaska southwards (Davies 1950, Sommerman et al. 1955, Stone and Jamnback 1955, Peterson and Wolfe 1958, Anderson and Dicke 1960, and Davies et al. 1962).

Ovipositing females were observed on beaver dams, sticks, stones, logs, cement embankments and vegetation dipping their abdomens in the water and laying the eggs in mats; up to seven females used the same spots (cumulative ovipositing), 1500 eggs were counted; often dead females were found stuck to these mats.

No mating swarms were encountered but all the females collected were fertilized. Females of the first generation emerged with their ovaries well developed (eggs in third stage) and the eggs in the laboratory reached maturity without the females mating or feeding; in the later generations there was a decrease in the ovarian development and females failed to develop their eggs without feeding. Fertilized females were collected from feeding swarms of S. venustum; attracted to the collector, females started biting on the neck and arm. Females were observed feeding on horses (June 14 - 17 1964, July 18 - 21 1965). Up to 70 flies were counted on a single horse at one time.

Simulium (E.) latipes

This is a holarctic species complex. In the palearctic it was reported that the overwintered larvae gave rise to a single generation a year and adults feed on cattle and humans (Davies 1952, Edwards 1920, Smart 1944, and Steward 1932).

In North America the species passes the winter in the egg stage, has one to three generations a year, feeds on birds, chickens, and man (Anderson 1956, Anderson and DeFoliart 1961, Bennet 1960, Davies 1950, Davies et al. 1962, Davies and Peterson 1956, Fallis 1964, Fallis and Bennett 1958, Hearle 1932, Hocking and Richards 1952, Peterson 1958, Shewell 1957, Sommerman et al. 1955, Stone and Jamnback 1955, and Stone 1964).

In the study area S. latipes has two generations per annum. The

overwintered eggs hatch in May and mature larvae and pupae appear between June 17 and 20 (1963-65). Commencing on August 17, pupae and mature larvae of the second generation were encountered in increasing numbers.

Females of this species emerged with no ovarian development (eggs in stage II - Christophers' classification 1960). Females induced to feed on chickens and yound sparrows failed to develop their eggs beyond stage III and died four days after a blood meal. Fertilized females netted in the field took blood meals from a chicken, a sparrow and the collector's arm, developed their eggs to maturity in 11 days but all died before laying. Davies and Peterson (1956) stated that S. latipes developed its eggs in captivity in 5 days at room temperature. Parous females took less than 11 days to develop their eggs in the second ovarian cycle i.e. it takes less time for each successive cycle due to the fact that the first blood meal is utilized in overall development of the gonads and the eggs. Other likely factors may be the decrease in the number of functional ovarioles and higher temperatures.

Simulium (S.) luggeri

S. luggeri is not a common species in the area. It breeds in the rapids and riffles of the Pembina river. The dates of pupation of the three annual generations are June 13 - 20, July 21 - 28 and August 26 - 26. Nicholson and Mickel (1950) described the species as having three generations in Minnesota, Fredeen collected pupae from mid June to

early July (the first generation) on the Canadian prairies; Hocking and Pickering (1954) collected pupae in northern Manitoba in August; Anderson and Dicke (1960) recorded two generations per annum in Wisconsin; Twinn (1936 as S. nigroparvum) described three generations of the species in eastern Canada (mostly from the Ottawa river, Ontario). S. luggeri passes the winter in the egg stage. Adults mated in small swarms near the breeding sites; fertilized females developed their first batch of eggs without blood meals but fed on horses and cattle before the second gonotrophic cycle. After that no females were encountered. Oviposition was not observed and no egg aggregations were detected, it is assumed that, since the known breeding sites yielded no eggs, the females scatter the eggs in the river.

Simulium (S.) tuberosum

Cytologically this Holarctic species was reported by Landau (1962) to consist of "four well defined breeding units and a likely fifth, all sympatric" in Ontario and with no evidence of hybridization. Davies et al. (1962) suggested the presence in Ontario of two or more undescribed forms of the species which are different from the Palearctic form of S. tuberosum.

Previous records revealed two to four generations a year (Smart 1944, Davies 1950, Sommerman et al. 1955, Stone and Jamnback 1955, Anderson and Dicke 1960, Davies et al. 1962). In the study area as elsewhere S. tuberosum overwinters as eggs. It has three generations per

annum: maturing larvae and pupae were collected on June 14 - 17, July 19 - 24 and August 20 - 24.

Larvae were seen to occur in dense mats on submerged surfaces of rocks and stones exposed to the sun in the Pembina and Athabasca rivers; they were usually well inside the stream and away from the banks.

Females required a blood meal for the first gonotrophic cycle and after mating they attacked cattle and were attracted to the collector in large numbers but only a few fed on my arms and legs and rarely on the neck or face.

Oviposition probably was on the surface of the water when the females were observed to descend from the air and settle on the water; eggs scattered in the water.

Larvae of S. tuberosum were closely associated with those of S. venustum. At low water larvae of the latter shared most of the substrates previously occupied by S. arcticum and S. tuberosum.

The last (third) generation was more abundant in the southern part of the study area than in the north.

Simulium (S.) verecundum

Separated from S. venustum in 1955 (Stone and Jamnback), this species proved difficult to study separately. Stone and Jamnback (1955) suggested two or three generations a year; Davies et al. (1962) found the same in Ontario. In the study area the collection of aquatic stages from

the Pembina river revealed a prolonged duration of larvae and pupae from May to August. This suggests three generations per annum. Adults were not attracted to the collector but were captured feeding on cattle.

Simulium (S.) venustum

This Holarctic species was second only to S. vittatum in abundance; aquatic stages were discovered in every breeding site and adults were regularly captured in the period May - September.

Stone and Jamnback (1955) questioned the value of the previous biological record of the species as a complex containing S. verecundum. They suggested that S. venustum has one generation annually (obligatory diapause). The S. venustum - S. verecundum complex was shown to have more than one generation resulting in a build up of an almost continuous population of adults in each season (Smart 1944, Davies 1950, Hocking and Richards 1952, Sommerman et al. 1955, Fredeen 1958 and 1960, Anderson and Dicke 1960 and Davies et al. 1962).

In this study three definite peaks were detected in the larval and pupal densities suggesting a three generation pattern for the species: The generation derived from the overwintered eggs is extremely large and reached a peak on June 10 - 17. The other two generations are smaller but they overlap to cover the rest of the season. Eggs are abundant as they are laid by females in mats sometimes twenty eggs deep and containing more than 1000 eggs. Females dive under water,

settle on water, vegetation, rocks, stones or logs and usually share an oviposition site together. Eggs were recovered easily up to September 20. July 10 - 15 and August 14 - 17 were the dates of pupation of the second and third generations respectively.

Females require a blood meal for the first gonotrophic cycle. Mating swarms were encountered and sometimes induced by the presence of the collector or the white top of a car. Females showed a definite preference for humans over cows and for cows over horses. After they land on a cow, a calf or a horse they are difficult to attract, but before landing they were observed to assemble towards a human host in the presence of other hosts. Females were collected feeding on a dog, on young sparrows and on pigs inside a barn.

Simulium (*P.*) *vittatum*

S. vittatum was the most abundant species in the study areas. Its aquatic stages were encountered in all the breeding sites examined. In the Athabasca river there was a noticeable decrease in the density of aquatic stages in the Hinton area but a gradual increase downstream (northwards).

Overwintered larvae were detected under the ice in the Pembina river, French, Chisholm and Blackmud (12 miles south of Edmonton) creeks. After the ice break-up the larvae of this species are predominant; they mature and pupate by May 11 to 13. Another peak of mature larvae and pupae was observed on May 28 to 30; this may be an emergence from

overwintered eggs. S. vittatum was reported to pass the winter in the larval and egg stages in Alaska (Sommerman et al. 1955), British Columbia (Hearle 1932, Saskatchewan (Cameron 1922, 1918), Ontario (Davies 1950), Connecticut (Stone 1964) and Wisconsin (Anderson and Dicke 1960).

Pupation of the second generation commences on June 25 to 28, of the third generation on July 27 to 30 and the last generation on August 24 to 29. Overwintering larvae were common in September. Anderson and Dicke (1960) reported the species to have four to five generations a year in Wisconsin; Davies (1950) reported two generations in Ontario; Davies et al. (1962) recorded S. vittatum as multivoltine in Ontario; DeFoliart (1952) assigned three or four generations to S. vittatum in the Adirondack Mountains (New York State); Fredeen and Shemanchuck (1960) found the species to pass through four generations in a season; Sommerman et al. (1955) recorded two and three generations of S. vittatum depending on the habitat; Stone and Jamnback (1955) reported three to four generations in New York; Stone (1964) reported one to five generations in Connecticut; Twinn (1936) described two to three generations in eastern Canada.

Females developing from overwintered larvae had well developed ovaries with the eggs almost mature on emergence. Mating swarms were observed from 1800 - 1900 hours; fertilized females from these were gravid five days later in the laboratory as also were females

reared from pupae and not mated. Ovipositing females settled on different substrates mainly well to the middle of the creeks and started depositing eggs in strings. The communal oviposition method was observed with four to seven females laying on the trailing leaves of vegetation. Females were collected later in the season, including those from overwintered larvae which had oviposited, feeding on horses and cows (mainly on the ear of the latter).

The females of this species were attracted to the collector in large numbers; they crawled inside the front of the shirt thus gaining access to the body. They started biting on the chest and the belly. Those outside the clothing started biting on the back of the neck and the arms. Females still feeding on cattle were carried inside the barns. They accumulated on windows where they were collected dead. Ants and spiders shared the daily crop of flies. Engorged females were seen flying under the barn lights at night. The preferred regions of feeding on cattle seem to be the ears and to a lesser extent the underside of the belly and the inside of the thighs. Only ear-feeding resulted in severe wounds. The swarming females are common; cattle and horses in the pastures are annoyed by these which are attracted to both moving and stationary objects. Females striking against the collector's face are inhaled and taken in the mouth.

Anderson and DeFoliart (1961) in Wisconsin and Wu (1931) in Michigan found the females to feed on cattle and horses but not to bite

man although they are attracted to him. Zoophilic and anthropophilic tendencies were reported by Cameron 1922, Davies 1950, Davies et al. 1962, Dyar and Shannon 1927, Hearle 1932, Hocking 1953, Jobbins-Pomeroy 1916, Jones 1961, Knowlton 1935, Knowlton and Maddock 1944, Malloch 1914, Sailer 1953, Shewell 1957, and Stone and Jamnback 1955.

HABITATS, HABITS AND SEASONAL PREVALENCE

EGGS

Simuliid females lay eggs in running water. There is no record of oviposition in stagnant water.

Cameron 1922, Edwards 1920 and O'Kane 1926 suggested that the eggs of some species of black flies (S. arcticum, S. latipes and P. hirtipes) respectively withstand desiccation. They may be subjected to this through water receding or the drying up of intermittent streams. Jobbins-Pomeroy 1916, Smart 1944 and Wu 1931 concluded from field observation and experimental evidence that the eggs are not resistant to desiccation. Fredeen (1959) devised a method for the extraction, sterilization and low temperature storage of black fly eggs collected from the field. He found that the eggs of arctic (and temperature) species overwinter and remain viable for longer periods in storage than the eggs of those species which pass the winter as larvae.

In this study, batches of eggs of Simulium venustum, S. vittatum and S. decorum were tested for desiccation resistance as follows: Egg batches were obtained from the breeding places and divided into three groups. The first group was used as a control and was firmly anchored or clearly marked in the breeding site. The second group was left on filter paper in the laboratory during the test periods (48, 144 and 264 hrs.) and then returned to water. The third group of eggs was used as a laboratory

control, covered by water in clean, open museum jars. The results are shown in Table 4.

The recorded (room) relative humidity was 67 - 74% and the temperature was 56 - 69°F. The eggs of these species need water for hatching and show no resistance to desiccation.

The Number and Dimensions of Eggs

Table 5 shows the average number of eggs laid by the females of ten species. The eggs of a batch mature at the same time but there are differences in the numbers of eggs laid within and between species. This was also recorded by Davies and Peterson (1956) for many species, in most genera. In a few species there is usually a decrease in the number of eggs in the second gonotrophic cycle. This results from degeneration of some ovarioles in which the eggs from the previous ovarian cycle were retained.

The simuliid egg is conical in ventral view and sub-triangular in lateral view. There is a bulge on one side of the egg and the side opposite that is the longest in profile.

Linear measurements were taken from the lateral view. The length was taken as the maximum measurement along the egg axis parallel to the longest side and the width dorsoventrally and perpendicular to this (Table 6). Davies 1950 and Davies and Peterson 1956 compared the dimensions of eggs of various species belonging to all the North American simuliid genera. The eggs of _Gymnopais_ and _Prosimulium_ were found

Table 4.

The progress of hatching of the eggs of
three simuliid species in relation to drying

Species	Field Control	Lab. Control	In air at R.H. 67 - 74%
S. vittatum			
48 hrs.	10% hatch	13% hatch	no hatch
144 hrs.	96% hatch	80% hatch	no hatch
264 hrs.	infected	infected	no hatch
S. venustum			
48 hrs.	48% hatch	35% hatch	no hatch
144 hrs.	87% hatch	88% hatch	no hatch
264 hrs.	100% hatch	94% hatch	no hatch
S. decorum			
48 hrs.	38% hatch	47% hatch	no hatch
144 hrs.	35% hatch	96% hatch	no hatch
264 hrs.	infected	infected	no hatch

Table 5.

Number of eggs per gonotrophic cycle in some species (including some previous published records)

Species	No. of Eggs per Female					Authority
	Max.	Min.	Mean	S.D.	No. of counts	
S. arcticum	162	-	135	-	-	Peterson 1959
nulliparous	204	123	165	±27.8	(22)	Present study
parous	177	116	139	±24.0	(20)	Present study
S. aureum	823	-	750	-	-	Davies & Peterson 1956
	810	686	745	±13.4	(21)	Present study
S. decorum	580	-	475	-	-	Davies & Peterson 1956
nulliparous	594	479	550	±51.0	(18)	Present study
parous	467	411	436	±20.7	(15)	Present study
S. latipes	312	222	275	±26.7	(16)	Present study
S. luggeri	174	135	154	±14.0	(12)	Present study
S. tuberosum	264	-	202	-	-	Davies & Peterson 1956
	-	-	225	-	-	Peterson 1959
nulliparous	218	234	227	± 7.4	(16)	Present study
parous	212	145	196	±17.0	(14)	Present study

Table 5 (cont.)

Species	No. of Eggs per Female					Authority
	Max.	Min.	Mean	S.D.	No. of counts	
S. venustum	553	-	455	-	-	Davies & Peterson 1956
	-	-	594	-	-	Hocking & Pickering 1954
nulliparous	572	465	513	±28.7	(16)	Present study
parous	511	441	481	±24.8	(15)	Present study
S. vittatum	395	-	312	-	-	Davies & Peterson 1956
nulliparous	398	363	380	±12.2	(17)	Present study
parous	311	254	285	±17.2	(16)	Present study
C. dacotensis	348	-	287	-	-	Davies & Peterson 1956
	288	276	281	±17.2	(16)	Present study
C. emergens	-	-	174	-	-	Davies & Peterson 1956
	211	125	163	± 26.0	(20)	Present study

Table 6.

Comparing the length and width of

mature eggs of some simuliid species

Species	Average length mm	Average width mm	Authority
S. arcticum	0.33	0.24	Cameron 1922
dissected	0.38	0.25	Present study
S. aureum	0.18	0.11	Davies & Peterson 1956
	0.21	0.14	DeFoliart 1951 (from above)
	0.19	0.14	Present study
S. decorum	0.25	0.14	Davies & Peterson 1956
	0.29	-	DeFoliart 1951
	0.27	0.16	Present study
S. latipes	0.22	0.14	Present study
S. luggeri	0.34	0.23	Present study
S. tuberosum	0.21	0.12	Davies & Peterson 1956
	0.21	0.11	Peterson 1959
	0.21	0.12	Present study

Table 6 (cont.)

Species	Average length	Average width	Authority
S. venustum	0.26	0.18	Davies & Peterson 1956
	0.25	0.18	Hocking & Pickering 1954
	0.25	0.16	DeFoliart 1951
	0.23	0.14	Wu 1931
	0.25	0.18	Present study
S. vittatum	0.26	0.16	Davies & Peterson 1956
	0.25	0.14	Wu 1931
	0.29	-	DeFoliart 1951
	0.26	0.16	Present study
Cnephia dacotensis	0.28	0.12	Davies & Peterson 1956
	0.27	0.14	Present study
Cnephia emergens	0.29	0.13	Present study

to be larger than these of *Cnephia* and *Simulium* except for *S. pictipes*, also the eggs of *Prosimulium* and *Cnephia* are narrow and eggs of other genera are sub-triangular in profile.

The angles, Table 7, were measured by an eyepiece goniometer.

Table 7

Measurements of egg angles of three simuliid species (in lateral view using eyepiece goniometer)

	Angles (degrees)								
	Head			Bulge			Third (tail)		
	range	mean	S. D.	range	mean	S. D.	range	mean	S. D.
S. venustum	35-55 (18)	45.5	5.9	89-101 (18)	95.6	4.4	41-55 (18)	49.0	5.6
S. vittatum	35-58 (9)	45.3	4.6	91-116 (9)	104.3	9.9	42-61 (9)	51.2	7.9
S. decorum	34-56 (11)	45.2	8.3	88-102 (11)	95.7	5.8	41-57 (11)	49.5	6.8

LARVAE

Breeding Sites

The simuliid larvae were found only in rivers and creeks. The young larvae of some species aggregate at the exits of creeks from lakes

and bogs. The older larvae are more evenly distributed downstream, and the mature ones are in the pupation sites which are in slow water and usually near the bank.

The head waters of the Pembina and the Athabasca rivers are at an altitude of about 3800 feet and the altitude is 2000 feet at Flatbush and 1690 feet at Athabasca town.

For about 4 to 7 miles down stream from big villages and towns there was a decreased population of simuliids. I attribute this to the influence of domestic and industrial waste disposal in the rivers. The creeks may be dammed for agricultural or industrial purposes for short or long periods during the season. Although they may be dry for some time, when there is a leak or overflow they get repopulated in the same season. Beaver dams are common in the area, usually giving rise to favourable breeding sites.

The chemical and physical analyses of the water in the two rivers and in the creeks gave closely similar results. The two rivers were slightly cooler than the creeks; Irish and French creeks were cooler than the others. The pH readings indicated low alkalinity in all the waters. It has been reported in the literature that black fly breeding streams are slightly alkaline (Anderson and Dicke 1960, Fredeen and Shemanchuck 1960, Peterson and Wolfe 1958 and Sommerman et al. 1955). Albeit Peterson and West (1960) mentioned that black flies can breed in water with pH 5.8 to 8.5: Anderson and Dicke 1960 recorded

pH values as high as 8.15 and 8.95 in Wisconsin. The dissolved oxygen concentration and the calculated saturated percentage showed fluctuations over 100%. Wu 1931, Petersen 1924 and Radzivilovskaya 1950, strongly upheld the theory that the function of the current is to maintain the oxygen saturation. Rubtzov 1939 and Zahar 1951 came to the conclusion that above a certain saturation there is no necessary requirement.

There were distinct differences in the composition and density of the vegetation in the various streams. Larval preferences were not clearly distinguished but it appeared as if whatever vegetation is present in the preferred locality within the breeding site is utilized as a substrate. Other factors affecting the selection are the nature of the bottom and the amount of exposure to sunlight.

The current velocity and flow volume varied considerably from one stream to another and within each stream.

The larvae of S. arcticum were limited in their distribution to the two rivers in the study area, albeit they have been collected from streams elsewhere (Fredeen 1958, Fredeen and Shemanchuk 1960) in southern Alberta, Peterson 1956 in Utah, and Sommerman et al. 1955 in Alaska). The current velocity was 1.5 to 5 ft/sec throughout the breeding sites except that mature larvae pupated in slower water near the banks of the rivers. The water was about three feet deep over the young larvae but only 8 to 14 inches above the pupae. Frequently pupae were exposed when the water receded; Equisetum stems are preferred

pupation sites as the plant grows near the water edge and in the water. The water temperature ranged from 32° to 61°F during occupation by the species collectively.

Closely associated with S. arcticum in the Pembina river was S. luggeri. The latter was sparsely distributed on the same substrata although stones and rocks were utilized especially for pupation. It was collected also from the lower reaches of French creek in similar positions.

S. tuberosum larvae aggregated on stones and vegetation exposed to the sun; the preferred current velocity was 0.6 to 3.5 ft/sec and the water depth was 3 to 18 inches. The species bred in the rivers and creeks.

S. verecundum, S. venustum and S. vittatum bred more in the creeks than the rivers; the Pembina river usually had a bigger population of aquatic stages per square foot than the Athabasca (Fig. 5). The current speed ranged from a trickle in one inch of water to about 5 ft/sec in more than three feet of water. The first two species appear when the temperature rises to 40°F.

S. decorum larvae were found to concentrate on shaded substrata in 3 to 12 inches of water and 0.5 to 1 ft/sec current. During the occupation of this species the temperature was 51 to 72°F.

The larvae of S. aureum were encountered only at above 50°F on trailing vegetation in streams with patchy vegetation growth in the water.

The preferred current velocity was 0.5 to 2 ft/sec in 5 to 12 inches of water. The maximum temperature was 71 F.

The distribution of the larvae of S. latipes indicated a discontinuity in the rivers and abundance in the creeks. The larvae were attached to the vegetation, sticks, and pebbles in the S. aureum breeding sites except that the temperature requirements were more eurythermic (starting from 40 F).

The larvae of C. dacotensis and C. emergens were collected from vegetation, logs, and bottom stones in 1.5 to 2.5 ft/sec current speed in one to three feet of water. The temperature was 38 to 51 F. The overwintered larvae of C. mutata were attached to the bottom pebbles and sticks in the same conditions.

Prosimulium decemarticulatum was well distributed in Irish and Flatbush creeks. The larval attachment substrata were dead or trailing vegetation, sticks, stones, and logs under 4 to 13 inches of water and 0.5 to 2 ft/sec of current. The water temperature reached 36 F before the larvae appeared.

Population Density Assessment

Two methods were employed in determining population densities. The first method was the direct counting of the numbers of larvae in a square foot of the river bottom. Two weekly collecting stations were selected in the Pembina river, one in the Athabasca river and one in each creek. Each station was about three miles long. A wooden frame

was applied to a selected (with suitable attachment substrata) area delimiting one square foot of the bottom and the attachment substrata of the simuliid larvae were investigated (average 8 sq ft counts). Bottom pebbles, debris, vegetation, sticks, stones, rocks and logs constituted the substrata (the last two usually encompassing more than one square foot). This method has been used in ecological studies and control assessments. Arnason et al. 1953, Anderson and Dicke 1960, Fredeen et al. 1953, Jamnback and Eabry 1962, Metcalf 1932 and Sommerman et al. 1955, Brown 1955, and Wolfe and Peterson 1959 used a five minute stone count in selected areas.

The second method was based on artificial attachment sites. These consisted of hollow, white, matt surfaced polystyrene-butadiene rubber ("high impact polystyrene") cones, 0.01 in. final thickness, 8 in. long, with a 4 in. base diameter and 30° apex, vacuum formed from 0.03" sheet by Spencer-Lemaire Plastics of Edmonton. One set of these was freely suspended by wire through the apices to wooden spikes fixed in the collection stations. Depth adjustment was attained by using cork or lead weights. Another set was fixed with the apices pointing upstream by fixing them to pegs through holes in the spikes. A similar method was employed by Peterson and Wolfe 1958, Phelps and DeFoliart 1964 and West et al. 1960.

In every collecting station there were control cones which were not changed during the season; but the others were checked and the larvae removed for counting every week.

Results

Although the projected area of the cone is only approximately 1/9th of a square foot, the number of larvae on a trailing cone was subequal to the number of larvae in a square foot of bottom. This may be due to attraction of simuliid larvae to bright objects or perhaps to the nature or shape or movement of the surfaces. This is supported by the finding that cones painted yellow, brown, red, green or blue yielded less larvae than the white cones (Table 8). Similar trends were observed by Wolfe and Peterson (1959) using painted parts of a spruce log.

The fixed cones gave very low numbers at all depths, the freely suspended cones had an optimum depth between 2 and 11 inches with a roughly inverse relationship between turbidity and optimum depth.

Peterson and Wolfe (1958) interpreted the population graph obtained in their study as representing three generations of all the species encountered in the period June to July with a small peak in May which resulted from the overwintered larvae and egg hatch (of all species) in spring. In my study area there was overlapping of the generations of one and all species whenever they were associated. This resulted in peaks in the population graphs (Figs. 2 - 7) corresponding to the life histories of more than one species in any station. For ease of comparison data have been adjusted in such a way as to synchronise the date of ice break up.

The spring peak depends on the abundance of the overwintered

larvae and eggs and the effect of winter on both stages. The high water of spring flood is of great advantage to the larvae as more substrata and organic drift are provided by the invasion of new areas. (Anderson and Dicke 1960, Carlsson 1964 and 1966, Fredeen and Shemanchuk 1960, Peterson and Wolfe 1958 and Philipson 1956 and 1957.) There are adverse effects of the high water as some of the larvae may be washed away and perish and there may be depositions of silt over the substrata.

The summer peak (or peaks) may result from the combined presence of the first generation larvae of those simuliid species with high temperature requirements, successive ovipositions of some species in the first generation and influx of larvae of the second generation. This may be prolonged until August and overlap the small fall generation.

Anderson and Dicke (1960) recorded 2000 to 4000 larvae/sq. ft. (300 to 800 larvae on a grass blade 0.5" wide and 6" long), Metcalf (1932) recorded 2880 and 1500 larvae on two rocks and 300 larvae/sq. ft, Peterson and Wolfe (1960) reported 2400 larvae/cone.

According to Hocking and Pickering (1954) the current gradient is important in the positioning of larvae on the substrata after the larvae attach. The fact that the cones suited the requirements of larvae is illustrated by the high catch recorded.

Fig. 2 Total population densities of simuliid larvae in the Pembina river:May to September 1963-1965

(adjusted for dates of ice-break up.)

Station 1

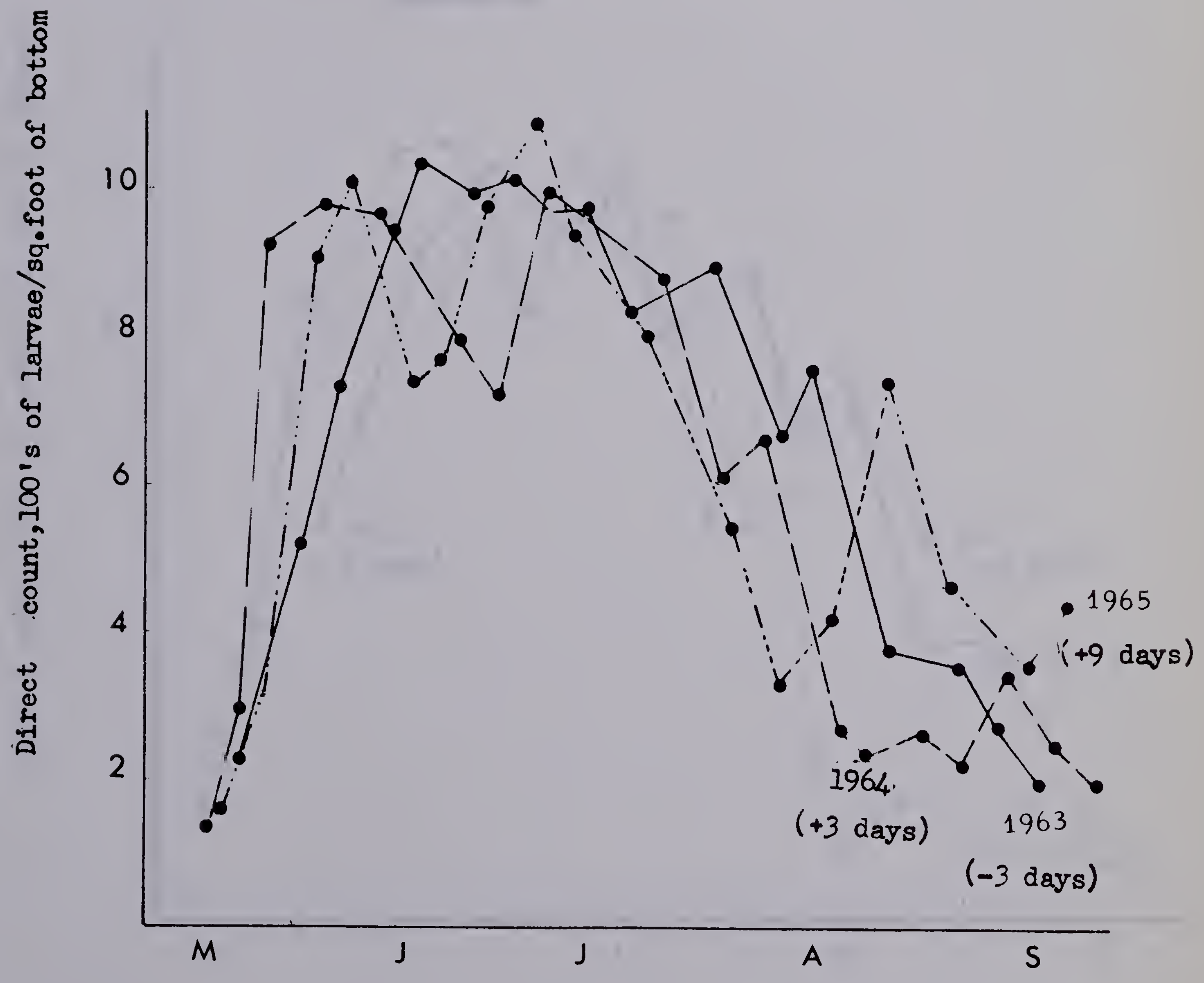


Fig. 3 Total population densities of simuliid larvae in the Pembina river:May to September 1963-1965 (adjusted for dates of ice break up.)

STATION 2

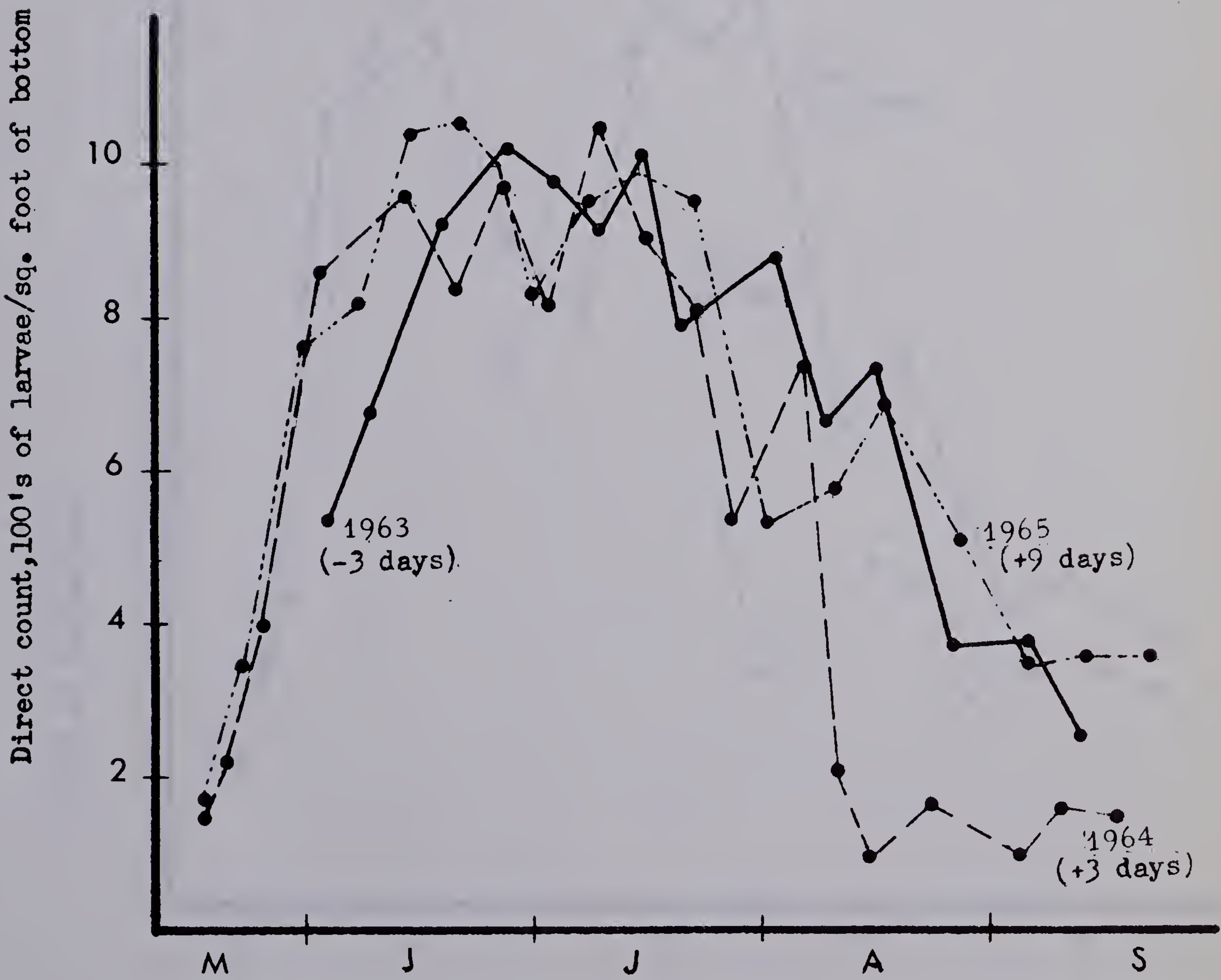


Fig. 4 Total population densities of simuliid larvae in the Pembina river: May to September 1964-1965. (adjusted for dates of ice break up).

STATION 1

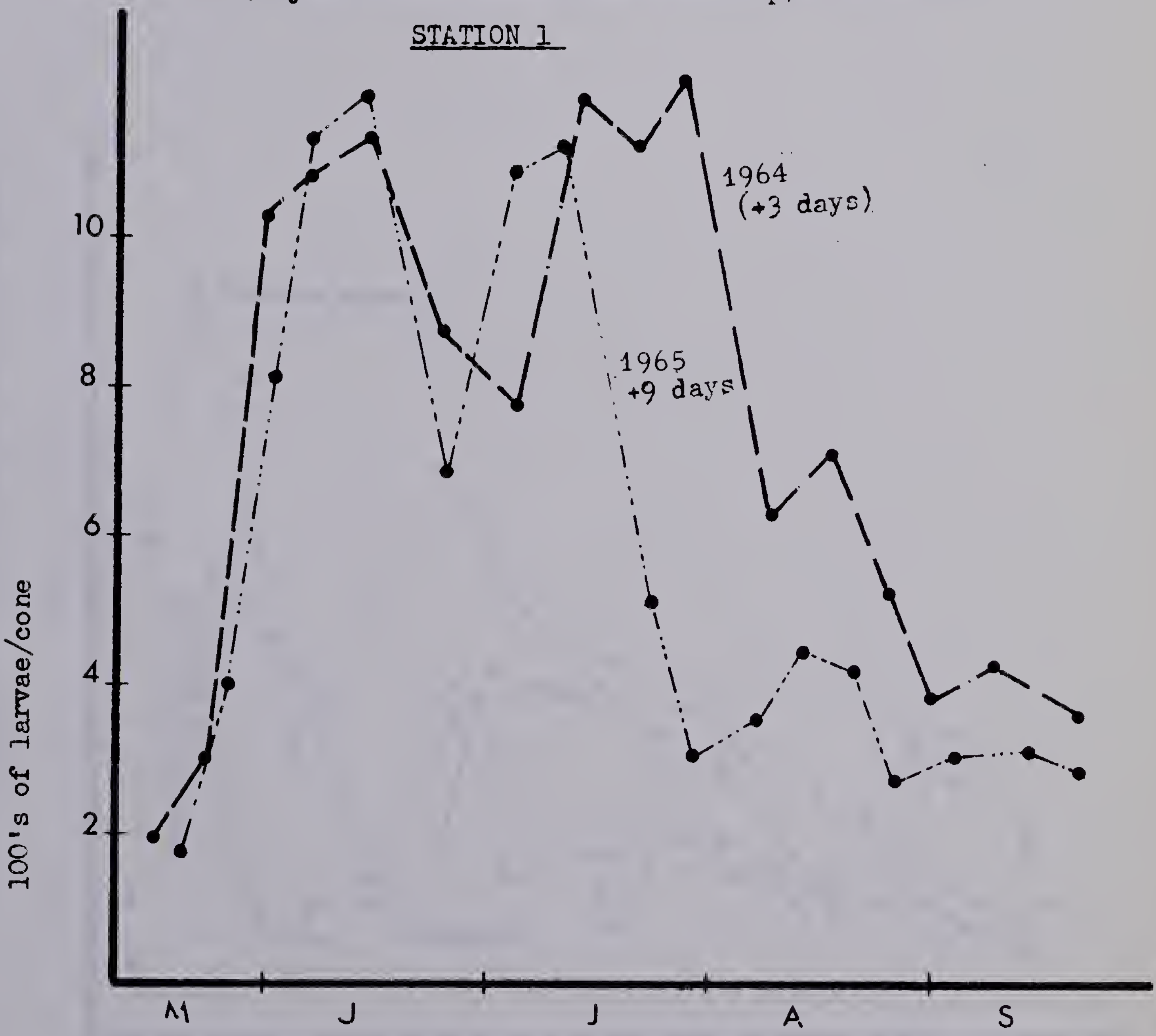


Fig. 5. Total population densities of S.arcticum larvae in the Athabasca(3 sites) and Pembina rivers 1965

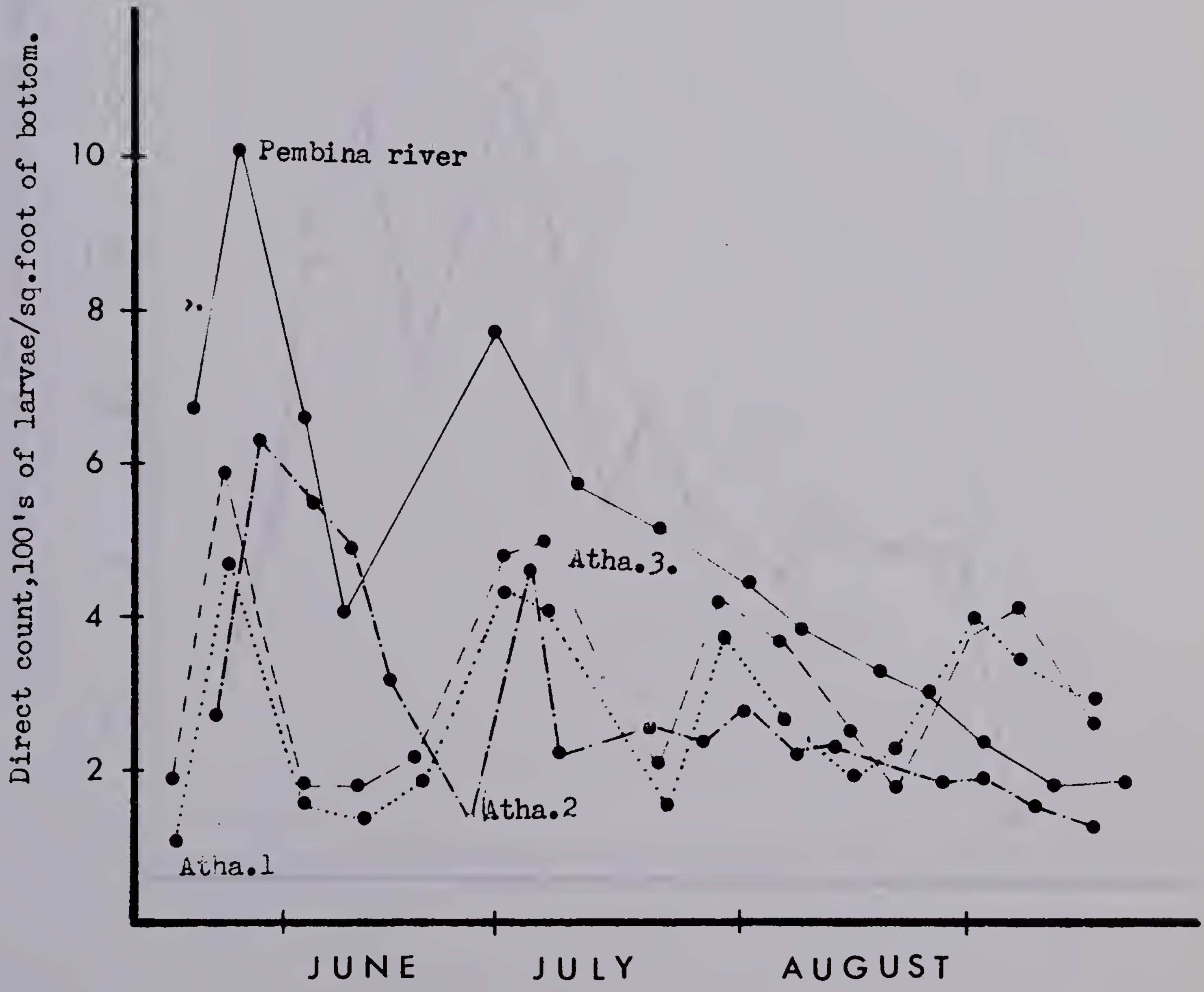


Fig. 6 Total population densities of simuliid Larvae in French creek: 1964

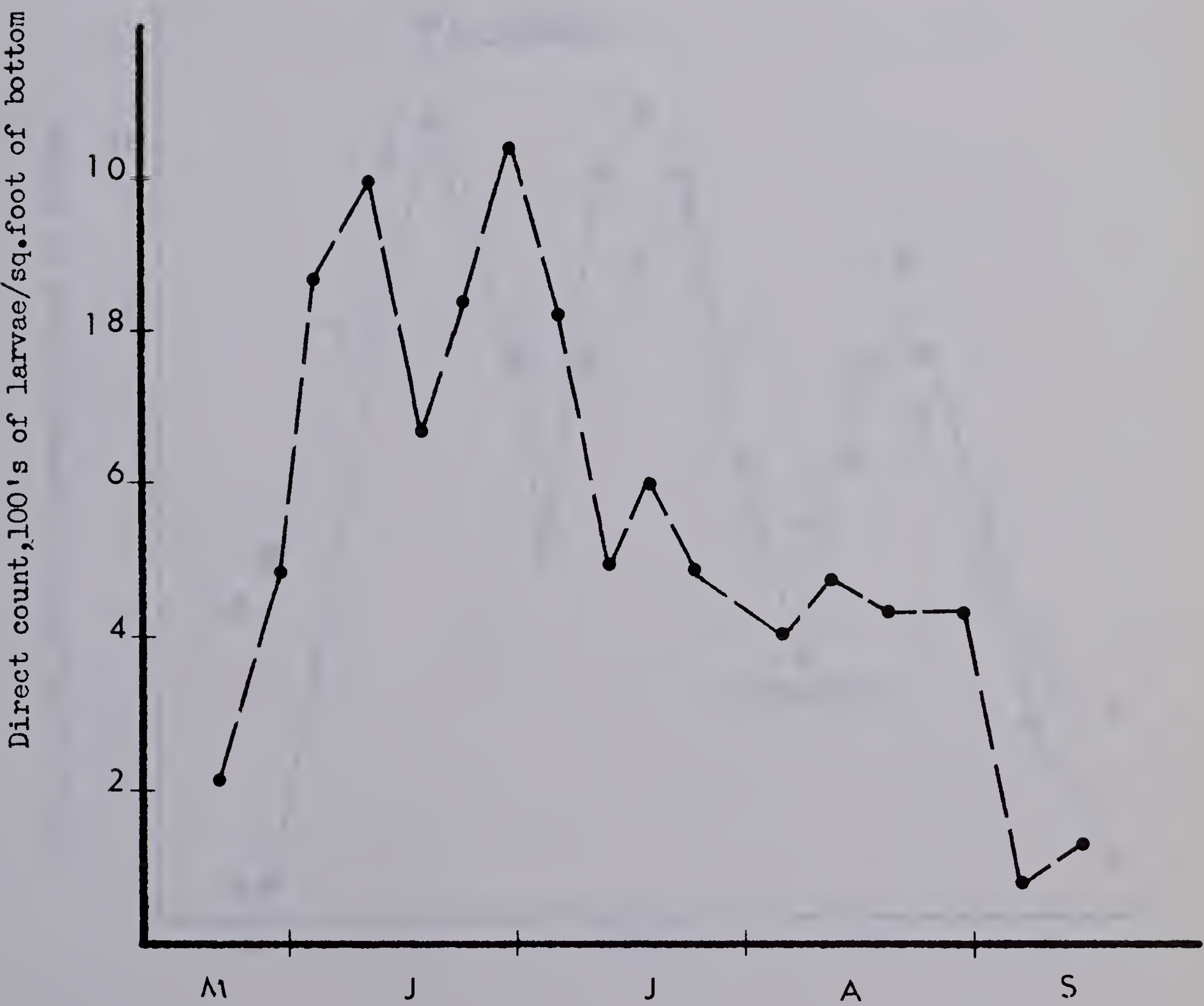
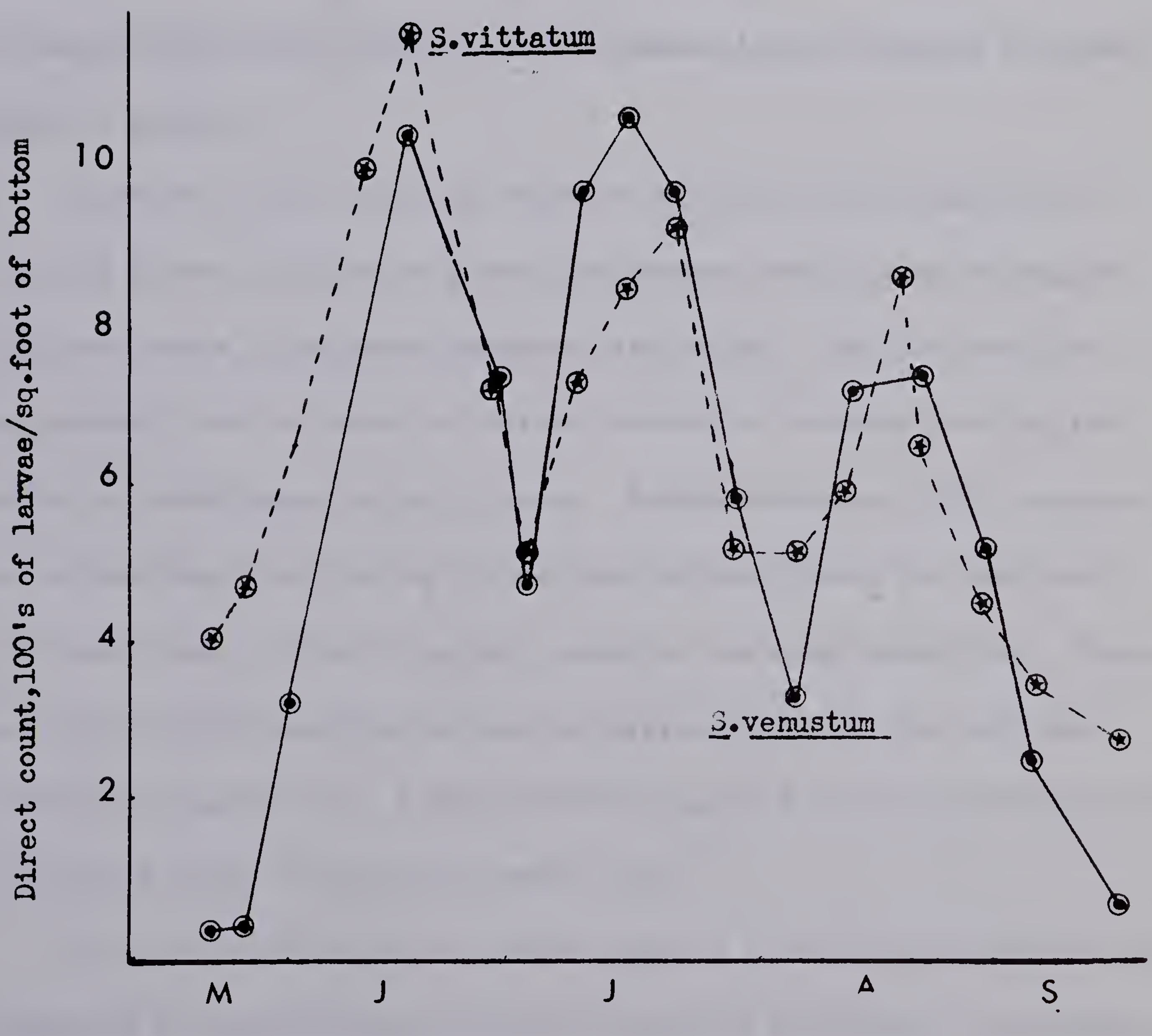
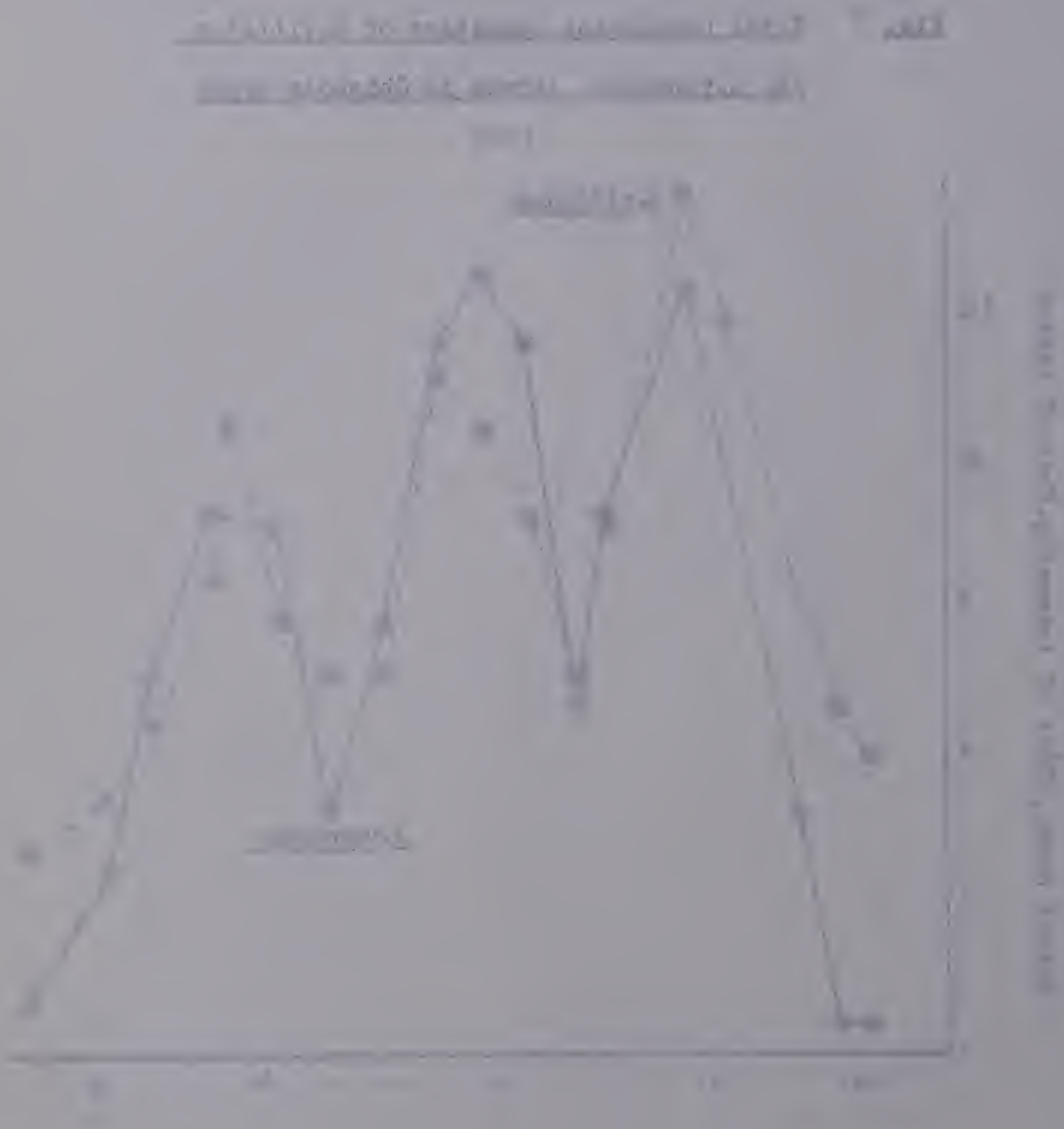


Fig. 7 Total population densities of S.vittatum and S.venustum larvae in Chisholm creek

1964





Larval Migration

The adult females fly upstream and oviposit, their eggs hatch and the larvae accumulate in these oviposition sites for short periods. They are passively carried downstream by the current. These young larvae were reported by Peterson and Wolfe (1958) to secrete silk threads to suspend themselves in the current. The larvae populate all the favourable breeding sites in the streams and the mature larvae migrate to slower water to pupate.

Rubtzov (1939) concluded from his studies on the migration of simuliid larvae that they migrate downstream continuously during the night and settle on different substrata in the day. He attributed the migration to the decrease in current velocity in one site inducing the larvae to seek higher velocity levels. Radzivilovskaya (1950) reported the larvae migrating during the day and settling during the night and attributed this to lowered oxygen content at the attachment site. Peterson and Wolfe (1958) reported the larvae migrating during the night and settling during the day. Yakuba (1959) suggested that migration may be stimulated by the rapid rise in water level.

The use of artificial attachment objects in studying migration was suggested by the application of plastic cones in the density assessments. The investigation suggests that the larvae migrate during the night in large numbers and settle on the cones after sunrise (Table 9). The larvae that released their grip and moved down stream during the day were too

few to constitute a category in the migration pattern. They may be dislodged by other larvae, drifting objects or as a result of the movement of the attachment object.

Flatbush creek was dammed in July 1963 and the bottom of the stream below the dam was dry. No eggs were found in June 1964, but the water overflowed the dam in July and continued to flow up to the end of the season. The stream was repopulated by simuliids in July and this was mainly done by females ovipositing below the dam and by larvae migrating from above the dam. In 1965 the simuliid populations in this creek was as high as in other creeks and the species of simuliids were: C. mutata, P. decemarticulatum, S. venustum, S. vittatum, L. latipes, and S. aureum.

Table 8

Numbers of simuliid larvae on plastic cones of different colours at different depths in the Pembina river, weekly collections, July and August 1965

Depth in inches:		2	4	6	8	10	12	14	16
Colour	Reflectance	Average number of larvae per cone/week (5 counts)							
white	0.5	147	181	386	634	943	858	900	154
yellow	0.3	8	14	11	8	-	-	-	-
green	0.1	17	57	48	31	31	60	94	46
brown	0.09	7	11	13	7	-	-	-	-
red	0.08	11	33	21	9	-	-	-	-
blue	0.07	13	34	59	43	76	87	88	97

Table 9

Average numbers of simuliid larvae picked up per cone in six hour periods (in the Pembina river, July and August 1965) (Mean of five observations)

Time:	6 to 12	12 to 18	18 to 24	00 to 6
	23	14	87	195

Rearing of Simuliid Larvae

Laboratory rearing of simuliid larvae was attempted by Fredeen 1959, Hocking and Pickering 1954, Mackerras and Mackerras 1948, Puri 1925, Smart 1934, Vargas and Dalmat 1951, Wood and Davies 1965 and Wu 1931. Only *Boophthora erythrocephala* de Geer has been reared from the pupa through two generations (Wenk 1963).

The methods employed were the use of compressed air to circulate the water in breeding jars, using stone or fritted glass air breakers and the movement of water: by the shaking or rotation of a platform carrying the breeding jars, by flow through tanks and troughs or by propulsion with propellers. The water used was chlorinated tap water, from aquarium tanks rich in algae or stream water. Rubtzov (1956) suggested that the maintenance of larvae in the laboratory may be facilitated by rearing them in water rich in micro-organisms. This was attempted by some workers; by supplying bakers' yeast, powdered skim milk and bacteria. At optimum temperature, oxygen saturation and current velocity, food was not an important problem in the laboratory rearing of simuliids.

In the present study two methods were successfully utilized in the study of life histories and other investigations.

Compressed air was bubbled into breeding bowls and museum jars. This method was found satisfactory in raising early stages of *S. venustum*, *S. vittatum* and *S. decorum* and for insecticide susceptibility tests. Larvae

were induced to attach on glass plates facilitating the change of water. As Hocking and Pickering (1954) suggested, autointoxication may be responsible for the mortality observed in jars after four to six days when the water was not changed. Fifteen to 30% mortality was recorded in 500 cc jars with less than 75 larvae; 40 to 80% in jars with more than 75 larvae. The average used was 250 larvae per 1500 cc bowl with the mortality increasing with increase in the number of larvae.

Two acrylic plastic troughs (described under susceptibility tests) were used in rearing efforts. These simulated breeding conditions in streams and the young larvae from the jars were transfered to the troughs and easily reared to pupae.

Water was collected from breeding sites and bakers' yeast was the only food added. The larvae of S. venustum were observed to scrape the aggregated yeast cells off the walls of the containers. Algal growth and microorganisms in the water were not removed.

Field investigations of nutrition were conducted by Anderson and Dicke 1960, Davies and Syme 1958, Hocking and Pickering 1954, Fredeen 1958 and 1964 and Peterson 1956. The larval gut contents yielded soil particles (sometimes 100%), organic debris : diatoms, algal filaments, spores, pollen grains, pieces of green and decayed vegetation and chitinous pieces of invertebrate body.

In the laboratory the larvae filled their guts with yeast cells, phytoplankton and other inorganic particulate matter. Starved mature larvae

emptied their guts in 9 to 17 days; 67% pupated and 12% survived for 21 days without filling their guts again. Larvae of S. vittatum without distinct visible histoblasts took 4 to 7 days to empty their guts and survived for 11 to 18 days.

The feeding process was as described by Hocking and Pickering 1954, Peterson 1956 and Osborn 1896. Internal fluid pressure and the current may be responsible for extending the fans. The fans were closed (drawn towards the mouth) two to 23 times in a minute. The secondary fan filaments may be employed to decrease the area between the filaments of the primary fan, thus enabling the larva to strain out smaller particles e.g. yeast cells.

Puri 1925, Peterson 1956, and Wu 1931 described cocoon spinning. The observed procedure agrees with previous descriptions except that the larvae of S. venustum, S. vittatum, and S. decorum took more than 60 minutes to finish the cocoon in the laboratory.

Association with other Aquatic Organisms

Jamnback and Collins 1955 and Jamnback and Eabry 1962 used standard nets to measure quantitatively the stream organisms, in relation to control. Other workers had listed the groups of organisms encountered (Anderson and Dicke 1960, Hocking 1950 and Hocking et al. 1949).

In the present study a 20 mesh per inch screen (5 x 5 feet) was used to investigate the association of simuliid larvae and other stream

organisms. The screen was fixed among the rocks in the breeding sites and supported by diagonal poles in the back. The collector worked downstream from a point about 100 yards upstream from the screen, disturbing the bottom substrata and turning stones and logs to dislocate the fauna which was trapped on the screen. The results are tabulated in Table 10.

No phoretic association was observed between the simuliid larvae and any other organism. At the start of the season and when the water levels were high the number of organisms was small but the populations built up following the rise in water temperature and decrease in flow which resulted in the formation of side pools in the rivers and areas of shallow flow in the creeks.

The crustaceans and snails were late-comers in each season while the other groups were usually present, in different numbers, in all stations all the season.

Table 10.

List of organisms associated with simuliid larvae

Mollusca

(Gastropoda)

(Pulmonata)

Annelida

Hirudinea

Helobdella _stagnalis_ Linn.

Theromyzon _occidentalis_ Verrill

Moorebdella _ferrida_ Verrill

Arthropoda

Crustacea

Daphnia sp.

Gammarus sp.

Insecta

Ephemeroptera
(nymphs)

Heptagenia sp.

Ephemerida sp.

Odonata

(nymphs)

Aeshna sp.

Agrion sp.

Plecoptera
(nymphs)

Nemoura sp.

Trichoptera

Limnephilus canadensis Banks

Brachycentrus occidentalis Banks

Helicopsyche borealis Hagen

Hydropsyche recurvata Banks

Hydropsyche sp.

Leptucella sp.

Athripsodes sp.

Polycentropus sp.

Mayatrichia sp.

Diptera

(Chironomidae)

Coleoptera

(Hydrophilidae)

(Dystiscidae)

Hemiptera

(Corixidae)

Chordata

Pisces

Esox lucius Linn.

Catostomus commersonii Lacepede

Pimephales promelas Rafinesque

Myoxostoma sp.

Simuliid Larval Susceptibility to DDT

Fairchild and Barreda (1945) investigated DDT as a larvicide against simuliid larvae in Guatemala and reported the effectiveness of the method. This led to further investigations and resulted in widespread black fly control for medical,veterinary and agricultural purposes (Africa: Barnley 1958, Brown 1962, Davies et al. 1962, Graham and MacHahon 1957, Wanson et al.1950, North America :Arnason et al. 1949, Gjullin et al. 1949 and 1950, Goulding and Deonier 1950, Hocking 1950, 1953, Hocking and Richards 1952, Hocking et al. 1949, Jamnback and Collins 1955, Jamnback and Eabry 1962, Kindler and Regan 1949, Peterson and Wolfe 1958, Peterson and West 1960, Twinn 1950, Travis et al. 1951 and West et al. 1960, West and Peterson 1960 and Prevost 1949; Central America: Lea and Dalmat 1954, Vargas 1945; Europe: Petrishcheva and Saf'yanova 1957 and Rubtzov, and Vlasov 1934).

Varous insecticides and formulations were investigated for the control of both aquatic stages and adults. Albeit eradication was not feasible spectacular results were obtained.

Laboratory studies were started by Lea and Dalmat in 1954 using screened tubes for containers and circulating river water through them. One and ten parts per million of toxicant in water were used. This method was adopted by the W.H.O. (WHO tech. Rep. ser. 87 (1954) pp. 21-24). 820 chemicals were investigated in the period Jan. 1952 to Jan. 1953.

Muirhead-Thomson (1957) reported on the reaction of the larvae in the laboratory to DDT and Dieldrin, using compressed air to circulate water in test jars.

Jamnback (1962) suggested two methods. The first method involves the use of a pump to circulate water in a reservoir pan to induce the larvae to detach from field substrata, insecticide exposure bags and then employing compressed air to circulate the water in the observation jars. The second method was reported by WHO 1964; it employs wooden troughs, the water circulated by a pump from a tank reservoir.

The above last method was modified by Travis and Wilton 1965 (a) and (b). They used V-shaped metal troughs for the tests and nylon bags to return the larvae to the stream for the observation period.

I used 500 cc museum jars fitted with glass plates (3.4" x 4"), compressed air and stream water. The larvae were introduced into the jars and left overnight to attach to the glass plates. After the larvae were selected and the jars were cleaned of excess larvae and substrata, the insecticide was introduced (solutions of DDT in ethanol added to the water to give the required concentration). The exposure time was one hour and after rinsing the jars to remove the insecticide, 500 cc of river water were added to commence the 24 hour observation period.

The tests were carried out at room temperature (63 to 67 F); the insecticide was supplied by the WHO in the mosquito larvae test kit (pp' isomer in ethanol). The % compositions of species tested were S.

vittatum 40%, S. venustum 30%, S. tuberosum 10%, S. decorum 10% and S. arcticum 10%.

Results are tabulated below.

The Troughs

Two plastic (acrylic) troughs approximately 6 feet long, 7.5 in. wide and 2 in. deep (corrugated transversely; the ridges one inch apart and 3/8 in. deep), were used as simulated breeding sites. The water circulated from a "baby" bathing tub (22 litres capacity) using a 3-gallons per minute discharge pump. One trough and one tub (reservoir) were used in the tests with insecticides the other was used for the control. It was found necessary to allow more time for attachment of larvae than the overnight period for the jars. It is easier to use the troughs as there is no handling of the larvae (usually a calculated risk). The disadvantage is the amount of water needed to conduct the tests and the large number of troughs required for a set of tests for various concentrations.

Calculated LC_{50} was 0.00213 ppm DDT (pp' isomer in ethanol) for one hour.

Table 11

Results of tests of susceptibility of

black fly larvae to DDT, Flatbush 1964 and 1965

Test no.	Concentration of DDT (ppm) .002	.004	.005	.010	.020	control (0)
Jar method						
1) 8.11. '64						
No. of larv. tested	50	50	50	60	70	70
% Mortality	40	80	80	100	100	0
2) 8.23.'64						
No. of larv. tested	70	80	75	70	65	75
% Mortality	50	100	100	100	100	0
3) 7.18.'65						
No. of larv. tested	65	65	65	60	60	65
% Mortaltiy	47	80	100	100	100	0
4) 7.23. '65						
No. of larv. tested	55	50	50	50	55	65
% Mortality	40	74	100	100	100	0
5) 8.7. '65						
No. of larv. tested	50	55	55	50	60	65
% Mortality	46	71	100	100	100	0

Table 11(cont.)

Test no.	Concentration of DDT (ppm) .002	.004	.005	.010	.020	control (0)
Trough method						
6) 8.8. '65						
No. of larv. tested	216	-	-	-	-	207
% Mortality	47	-	-	-	-	0
7) 8.10. '65						
No. of larv. tested	-	194	-	-	-	203
% Mortality	-	83.3	-	-	-	0
8) 8.13. '65						
No. of larv. tested	-	-	211	-	-	253
% Mortality	-	-	100	-	-	4.4

Percentage mortalities corrected by Abbott's formula.

PUPAE

Pupae of P. decemarticulatum were recovered mainly from the bottom sand of Irish creek and in the laboratory the mature larvae pupated in the bottom of the rearing bowls where they spun loose cocoons. Pupal aggregates were encountered in vegetation, rocks and other substrata located in slow and shallow water. Peterson (1959) suggested that there may be a positive thigmotrophic response facilitating the pupal development. Stranded pupae of S. arcticum, S. decorum, S. venustum and S. vittatum were observed exposed above the water level as a result of a drop in water level, in some cases the pupal mass was kept moist by the fine spray from the water splash but when dried the pupae perish.

Carlsson (1966) indicated that each species has a certain pupal optimum temperature but the range between the maximum and minimum developmental temperatures is broad. In the laboratory I noticed that the duration of the pupal stage of S. vittatum, S. venustum, S. decorum and S. arcticum (obtained from the same batch of mature larvae of each species) took from three to eleven days, and that the position of the pupa in the mass did not influence its duration; but,as in the field observation, the emerging adult may be trapped under the pupal mass and perish. Organic and inorganic drift sediment piling above the pupal mass may interfere withthe emergence of the adult. Rubtzov (1956) indicated that there is a correlation between the number of pupal respiratory filaments and the character of the stream in relation to oxygen supply i.e. pupae

in swift water have less filaments than those in slow current. I found that _S. latipes_ with four filaments breeds in the same stream as _C. dacotensis_ which has numerous filaments, _S. vittatum_ with 16 filaments and _S. venustum_ with 6 filaments. Pupae kept in vials with moist cotton pads matured in less time than others of the same group left in the breeding troughs.

The adult emerged through a longitudinal split on the dorsal surface of the pupal skin pushing its thorax first followed by head and swiftly rising in a bubble of gas to the surface where it took off or was carried by the current to the nearest support.

ADULTS

Various methods have been used in studying populations of adult simuliids. Davies (1950), Davies and Syme (1958), Hocking and Richards (1952) and Ide (1940) used emergence traps. Light traps were employed by Davies (1955), Davies and Williams (1962), Fredeen (1961) and Williams (1948). The baited trap was preferred by Anderson and DeFoliart (1961), Bennett (1960) and Fallis and Smith (1964). Fredeen (1961) utilized "silhouette traps" which consisted of wooden frames in shape of animals (cow, sheep and horse) and covered by cloth of appropriate colour to match the animal it represents. Hocking and Richards (1952) and Davies (1961, 1963) applied sweep-netting and fly-boy-hour counts. The latter method was recommended by the World Health Organization in relation to control.

I used a light trap (ultra violet) in the period July to September 1963 and June to August 1964, at the field station (4 miles from the river); the total catch was: 91 female _S. venustum_, 49 female _S. decorum_, 36 female and 24 male _S. arcticum_ and 18 female _S. latipes_. This represents a low yield compared to some records by the above workers.

Nylon gauze and paper coated with castor oil and sticky traps (tanglefoot and fly paper) were hung near bird nests and on vegetation near the breeding sites. The adults caught were utilized in the life histories studies. Quantitative study of the abundance of adult simuliids was attempted by sweep netting of flying, feeding, and resting flies; the average number of flies in ten sweeps is plotted in Figure 8.

The diurnal activity pattern consisted of a peak of activity two hours after sunrise and a peak starting from two hours before sunset and continuing until after dark. The latter peak was more conspicuous as it consisted of many species and more individuals than the former.

The emergence pattern of the adults was investigated in the laboratory and the field using emergence cages (20 mesh per inch nylon screens). The investigation was on _S. vittatum_ in July 1965; approximately 100 pupae were selected from the breeding site for each period (two hour observation); to obtain pupae of the same age dark coloured individuals were used. In general agreement with the published data, the observed adult emergence in the field was between 5:30 a.m. and

1:30 p.m. In the laboratory it commenced two hours before sunrise and reached a climax at 9:00 a.m. but continued throughout the rest of the day in a random pattern.

<u>Fig.</u> 8 <u>Populations of adult simuliids,all species(sweep-netting) Flatbush,1964 and 1965.</u>

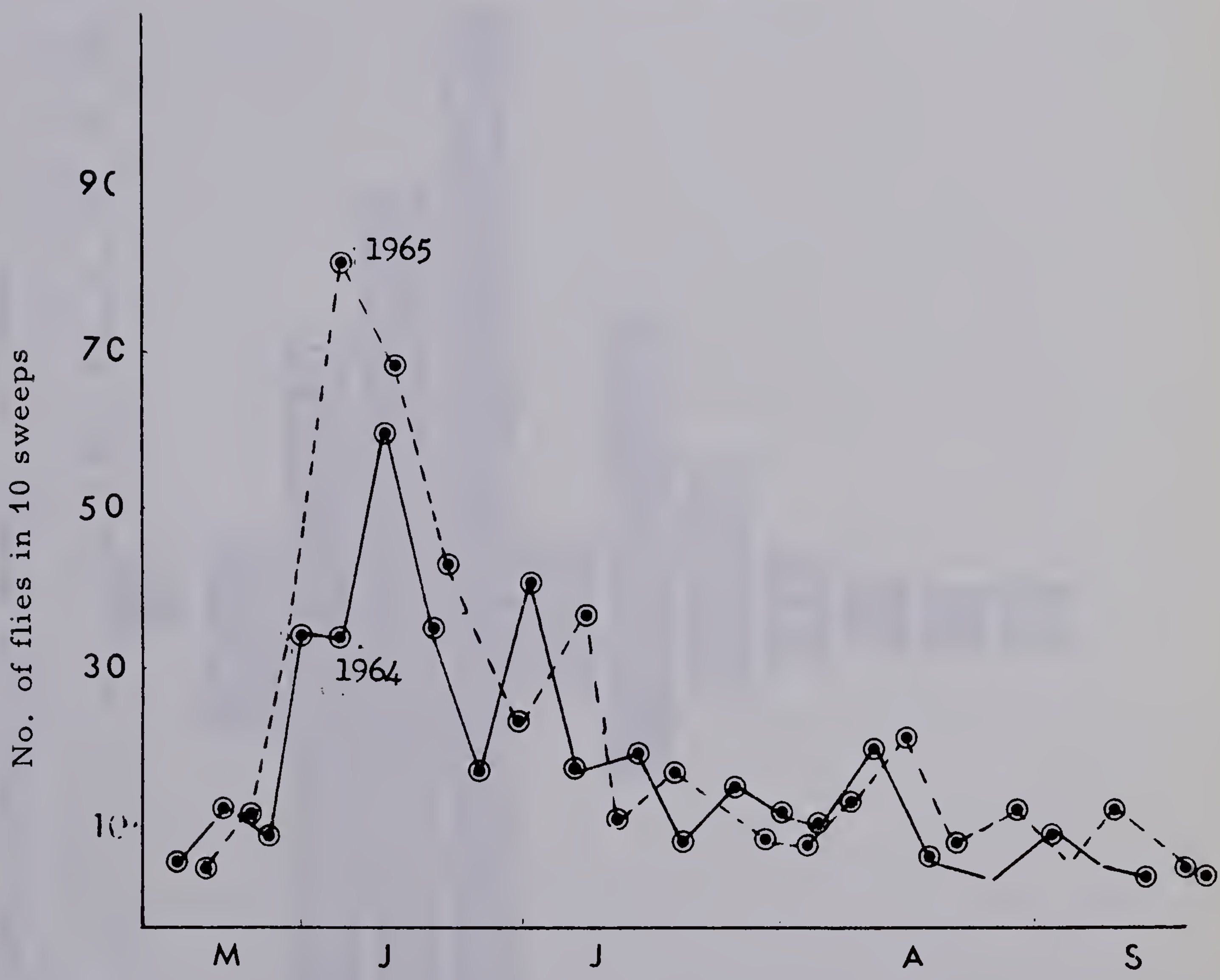
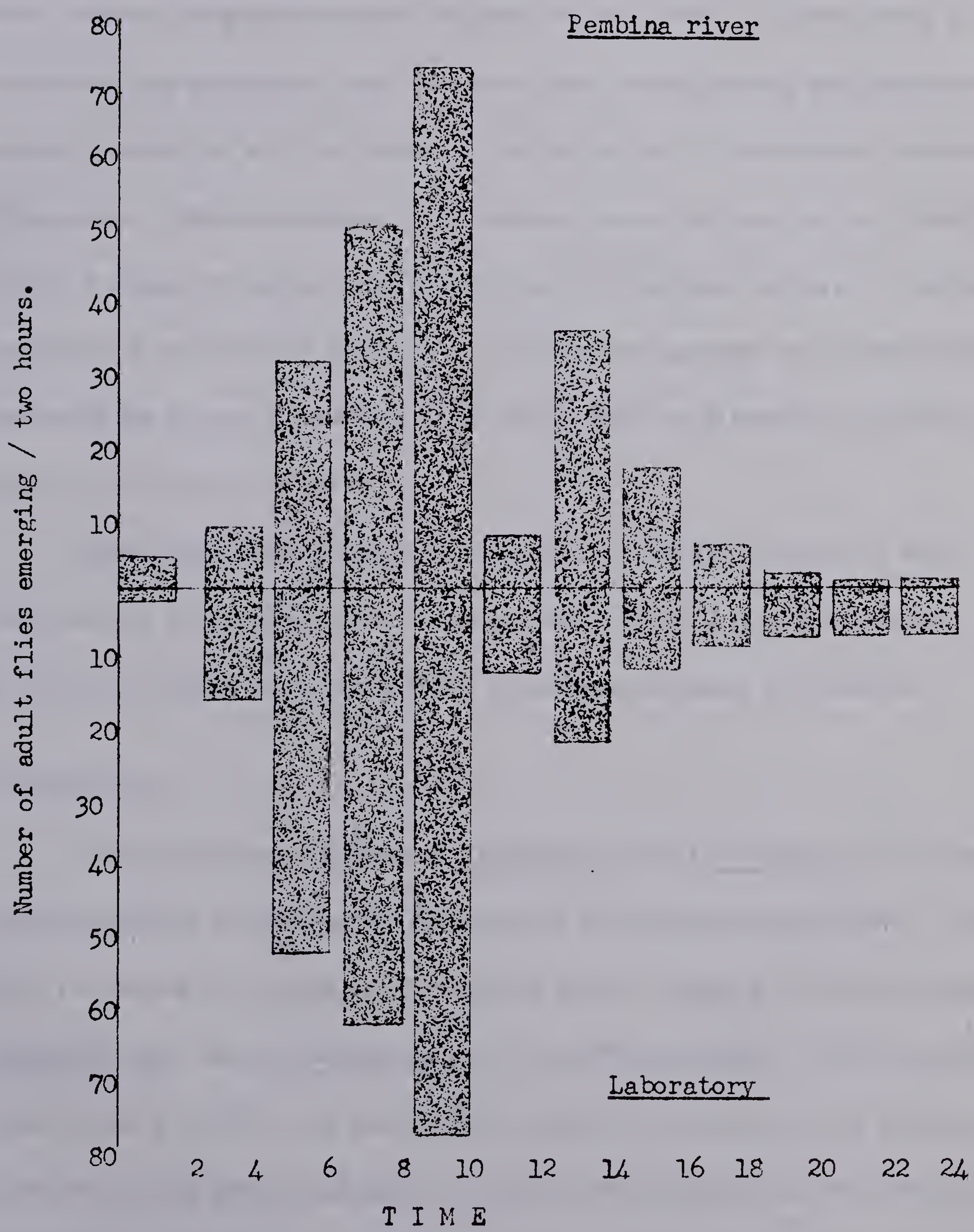


Fig. 9 **Adult S.vittatum emergence pattern**



BIOTIC CONTROL

PREDATORS

Predation on adults was not studied. The larvae associated with other stream organisms were accessible for study. In the study it was observed that predators play a minor part in regulating the numbers of larvae present at any one point. The larvae of Trichoptera, nymphs of Plecoptera, Ephemeroptera and Odonata were limited in their distribution within a single breeding site and therefore they had access to limited populations of simuliid larvae. Yet the above groups were positively recorded as larval predators when their guts on dissection yielded whole larvae or remains of larvae.

Other important groups consisted of leeches, birds and fish. The leeches increased in the creeks, especially late in the season, and the fish and birds were uniformly scarce throughout the season.

PARASITES

The two protozoan genera *Thelohania* and *Caudospora* (Protozoa: Microsporidia) are the most common of the simuliid parasites. Davies 1957 recorded *T. bracteata* Strickland and *T. fibrata* Strickland from *Simulium* spp. and *Caudospora* sp. from *Prosimulium*. The infection rates were 4 to 36%. In the present study the infection rate with microsporidians was estimated as 27 to 33% in the creeks and 0 to 45% in the Pembina and Athabasca rivers.

It was observed that the infection with these parasites increased in the second generations but decreased rapidly in the middle of August and did not recover again until the end of the season. Adult infection was highest in May - June (2 to 8%).

Nematodes

Mermithid nematodes are parasites of invertebrates and Welch (1963) collected 153 world records of simuliids parasitized by species belonging to the five aquatic genera: Isomermis, Limnomermis, Gastromermis, Mesomermis and Tetradonema. Rubtzov 1964 reported simuliid parasitism by sphaerularids (Nematoda : Sphaerularidae) in Russia.

The overwintered larvae of S. vittatum had infection rates of 7 - 47%, mean 26.1% (22 samples from seven localities in 1963 - 1965 seasons). The only species of mermithid parasitizing these larvae was Gastromermis viridis Welch. A single record of 79% infection was obtained in a sparce population in Chisholm creek, on July 22, 1964. Other species breeding in the same locality were not infected.

S. venustum was infected by Mesomermis flumenalis Welch. The infection rates were 35 to 64%, mean 45.1% (approximately 89 samples from about 7 to 13 sites per season : 1963 to 1965). Sparse and isolated populations of this species, especially in the creeks and the Pembina river, reached 94% infection rates.

S. arcticum, S. aureum and S. tuberosum were infected at very low rates. Their parasites were Limnomermis sp. Pupal and adult

infections were estimated as 14 to 23% and 7 to 9% respectively (calculated on the basis of total collections: 1963 - 1965).

In the laboratory seven females and four males of S. vittatum (raised from infected larvae) emerged in July 1964 with nematode infections.

The above data indicate that the parasites are specific, infected larvae were retarded (metathetely), most of them died and pupal and adult infection contributed to the infestation of the upper reaches of the streams.

Dr. H. E. Welch kindly helped with the identification of the mermithid nematodes.

DISCUSSION AND CONCLUSIONS

The 15 simuliid species recorded in this study represented the common species in central and central western Alberta. The study area extended from the southern limit of the boreal forest, and the northern boundary of the Parkland to the eastern edge of the boreal cordilleran vegetation region (Moss 1955).

The seasonal variations in the dates of ice break up, river discharge and weather conditions were slight in 1963 and 1964 but 1965 records of river discharge were higher than the average. But it seemed to be without adverse or favourable effects on the populations of the aquatic stages.

The systematics of the family are not clearly outlined. *Cnephia* overlaps *Prosimulium* and *Eusimulium* (subgenus of *Simulium*). The two new genera: *Paracnephia* Rubtzov and *Crozetia* Davies were erected to accommodate species included in *Cnephia* (in the Ethiopian region). The same problem of *Cnephia* species exists here. The lack of distinctive morphological characteristics at the species level resulted in the species complexes encountered in the simuliid fauna here. Cytological investigations revealed the presence of distinct forms within the species of many genera, in the Arctic and Palaearctic simuliids.

The slight variation in the species life histories was directly related to the environmental conditions under which the aquatic stages

developed. The presence and absence of the different forms of a species might have contributed to these differences and to the marked dissimilar reports of the life histories in the literature. These reports concern the number and timing of the generations, and the abundance of the species.

S. vittatum underwent no diapause while the univoltine species: C. dacotensis, C. emergens, C. mutata, and Prosimulium decemarticulatum, and probably P. onychodactylum and P. travisi underwent obligatory diapause. The other species were facultative with the eggs only overwintering, but no indication of summer aestivation was observed.

The species distribution followed their habitat preferences. The riverine species were the most restricted e.g. S. arcticum, S. luggeri and to a less extent S. tuberosum. The rare species P. onychodactylum and P. travisi were collected at altitudes over 3000 feet. Other species were widely distributed in the area.

Mating swarms were not commonly observed but the females attracted to the collector, to other animals, moving objects, and in bird nests were fertilized. It is suggested that mating precedes blood feeding; this may be the reason why many species failed to feed in the laboratory, as they did not mate in captivity. It follows that parthenogenetic species should be easily induced to feed and oviposit. Two species (Boophthora erythrocephala DeGeer and Wilhelmia salopiensis Edwards)

are now known to mate, feed and oviposit in the laboratory (Wenk 1963, 1965). The oviposition of females in captivity has been reported by some workers but it was not frequent.

C. mutata was the only parthenogenetic species in the area, cytological investigations (Basrur and Rothfels 1959) revealed the presence of both the triploid (parthenogenetic) and the diploid bisexual forms in Ontario. Only females were captured in the 1965 season in the study area but a few males were bred out of pupae collected in 1963 and 1964.

Autogeny was exhibited by univoltine species with weak mouth parts which are incapable of piercing the vertebrate skin, e.g., C. dacotensis and C. emergens; females of the former had their eggs almost mature on emergence, the females of the latter species had much stored nutrients and eggs were only half developed. Other species (S. arcticum, S. vittatum, and S. decorum) were autogenous in the first gonotrophic cycle in the first generation, taking a blood meal for the second ovarian cycle in the first generation and for the first cycle in the subsequent generations. Fredeen (1963) observed that S. arcticum females accumulate after oviposition in the first generation and attacked in swarms under favourable weather conditions to obtain a meal for the second gonotrophic cycle.

The third group of females were anautogenous. These were characterized by the large number of eggs in each ovarian cycle, usually laid in masses. These build up large populations of larvae in the breeding sites. (S. venustum, S. aureum, S. latipes and P. decemarticulatum.)

This crowding led to competition among the larvae for food and substrata, and might have contributed to the lack of stored nutrients carried over to the adult stage. Lack of stored nutrients could be also interpreted by the quality and quantity of food available to the larvae, the morphology of the cephalic fan (spacing of the filaments) being an important factor. The adult feeding habits of these females indicated no preference. Mammalophilic S. venustum fed on 5 different hosts, including a sparrow; the other 3 species fed on different bird hosts. They were at an advantage as they were not exposed to the risks of long flights. Securing a blood meal with such ease contributed to the longevity of the females and ensured repeated ovarian cycles.

The larval development commenced before the growth of the vegetation but the species differed in their developmental thresholds of temperature. These differences occurred in all generations of all species in each year. The overwintered larvae have low and the overwintered egg (embryo) have high temperature requirements.

The seasonal prevalence of the different species indicated by the total population densities of the larvae in the rivers and creeks did not show much fluctuation in the last three years. In June 1965 there was an apparent reduction in the total larval population which could be due to the effect of adverse weather conditions on the adult population of S. arcticum, and other riverine factors.

Larval migration downstream from upstream oviposition sites as

well as the influx of migrant females accounted for the repopulation of streams. Predators and parasites would migrate or drift downstream also. In the case of those species that lay their eggs singly (scattered eggs) there is a possibility that the eggs drift or are washed downstream by the current. Migrating larvae secrete a silk thread (up to three feet long), to which they attach while suspended in the current, thus securing themselves against drift. It has been reported that insecticides in the stream induce the larvae to release their grip and be carried downstream where they perish. In the present study, laboratory tests of susceptibility of the larvae to DDT indicated the extreme toxicity of the insecticide to the larvae; calculated LC_{50} was 0.00213 ppm DDT for 1 hour (pp' isomer in ethanol). Similarly, high mortalities resulting from field applications and laboratory tests with low doses of insecticides have been reported.

Laboratory rearing of simuliids ended with the emergence of the adults from the pupae. As Wenk (1965) reported, the problems involved were: mating, feeding and oviposition in the laboratory, and these difficulties were overcome with the discovery of two laboratory mating species in Europe. All other species fed on blood developed sterile eggs and oviposited without mating. Eggs dissected out of wild gravid mated (fertilized) females did not hatch. The latter phenomenon suggests that eggs are fertilized in the common oviduct prior to oviposition.

Emergence of aquatic as of many other species follows a diel periodicity, e.g., chironomid pupae (Palmen 1958), gall midges (Barnes

1930) and <u>Drosophila</u> (Brett 1955). Davies (1950) studied the factors that affect the emergence of adult simuliids. There was general agreement that light intensity was the main stimulus and that emergence was temperature independent, although the temperature exerted some control on the hourly emergence. I observed that in the laboratory there existed an attenuated emergence between 10 pm and 3 am (two hours after sunset to about an hour before dawn). In the field the adult yield in the emergence traps dropped considerably after sunset and did not recover except at dawn. The variations in these emergence patterns are likely due to temperature fluctuating less indoors than in the stream, or lights on at night. Temperature may be responsible for initiation of emergence.

Adult activity observations revealed a diurnal periodicity. There were two peaks of flight activity; the first commenced about two hours after dawn, continued for three hours after sunrise and the second occurred irregularly two to three hours before sunset and for sometime in the night. The same pattern of activity was described by Davies (1957) for <u>S. ornatum</u> Mg. Davies (1963) and Wolfe and Peterson (1960) reported on studies on the nulliparous and parous females concluding that parous females tended to fly in the late afternoon. Lewis (1958, 1960) observed <u>S. damnosum</u> to fly at noon. My studies were on <u>S. venustum</u>, <u>S. vittatum</u>, <u>S. arcticum</u> (mammalophilic species), and <u>S. latipes</u> and <u>S. aureum</u> (ornithophilic species). Sweep-netting near the breeding sites yielded a large number of nulliparous and a few gravid females and males. The population

composition of females on the wing was varied. The emergence of the adults of a species of any of the above groups changed the age composition of the flying simuliids. Nulliparous females were dominant at the beginning of the season (late May and early June). The number of flies eventually decreased, and the parous females outnumbered the nulliparous. This pattern continued throughout the season.

This diurnal activity was influenced by the daily weather and meteorological conditions as reported by Dalmat (1954, 1955), Davies (1952), Davies (1957), Wolfe and Peterson (1959, 1960), Wenk (1963, 1965), and Zahar (1951), which indicated a similarity in different regions. In the present study no species exhibited any preference for any set of conditions but there was a uniformity in abundance in both periods of activity with a slight increase in numbers in the afternoon-evening peak. The low light intensity, moderate wind and high relative humidity were the main factors concerned and these were fulfilled in the above periods.

Biotic control agents of simuliids included mermithid nematodes, microsporidians, and predators. The value of Gregarinida (Sporozoa : Protozoa) was not investigated as these parasites were not very common. Microsporidian infections were fatal to the larvae and adults but their importance as biotic control agents of simuliids was not definite. The low incidence of infection with this parasite suggested a secondary value. On the contrary, the mermithid nematodes were efficient parasites reaching 94% in some larval populations (although it may be said here

that infected larvae were slow to migrate and to pupate and this led to isolations of these populations which resulted in the high rate of infection observed). Host specificity of the nematodes was significant and was considered a disadvantage. The value of the predators (on the aquatic stages) might not exceed that of the microsporidian infection.

REFERENCES

Agassiz, L. 1850. Black flies. Gould, Kendall and Lincoln, Boston. pp. 34-35, 42, 52, 55, 61-62, 79 and 115.

Anderson, J.R. and R.J. Dicke. 1960. Ecology of immature stages of some Wisconsin black flies (Simuliidae : Diptera). Ann. ent. Soc. Amer. 53 : 386 - 404.

Anderson, J.R. and G.R. DeFoliart. 1961. Feeding behavior and host preference of some black flies (Diptera : Simuliidae) in Wisconsin. Ann. ent. Soc. Amer. 54 : 716 - 729.

Anderson, J.R. and G.R. DeFoliart. 1962. Nematode parasitism of black fly (Diptera : Simuliidae) larvae in Wisconsin. Ann. ent. Soc. Amer. 55 : 542 - 546.

Anderson, J.R. and G.H. Voskuil. 1963. A reduction in milk production caused by the feeding of black flies (Diptera : Simuliidae) on dairy cattle in California, with notes on the feeding activity on other animals. Mosquito News 23 : 128 - 131.

Anderson, J.R., D.O. Trainer and G.R. DeFoliart. 1962. Natural and experimental transmission of the water fowl parasite, Leucocytozoon simondi M. and L. in Wisconsin. Zoonoses Research 1 : 155 - 164.

Anderson, R.C. 1956. The life cycle and seasonal transmission of Ornithofilaria fallisensis Anderson, a parasite of domestic and wild ducks. Can. J. Zool. 34 : 485-525.

Anderson, R.C. and A.M. Fallis. 1955. Black flies (Simuliidae) as vectors of _Ornithofilaria fallisensis_ Anderson. J. Parasit. 41 : 45.

Armitage, K.B. 1958. Ecology of the riffle insects of the Firehole river, Wyoming. Ecology 39 : 571-580.

Arnason, A.P., A.W.A. Brown, F.J.H. Fredeen, W.W. Hopewell and J.G. Rempel. 1949. Experiments in the control of _Simulium arcticum_ Malloch by means of DDT in the Saskatchewan river.

Barnes, H.F. 1930. On some factors governing the emergence of gall-midges (Cecidomyidae : Diptera). Proc. Zool. Soc. Lond. 1930 : 381-393.

Barnley, G.R. 1958. Control of _Simulium_ vectors of Onchocerciasis in Uganda. Proc. 10 Int. Congr. Ent., Montreal, 1956. 3 : 555-537.

Basrur, P.K. 1959. The salivary gland chromosomes of seven segregates of _Prosimulium_ (Diptera : Simuliidae) with a transformed centromere. Can. J. Zool. 37 : 527-570.

Basrur, P.K. 1962. The salivary gland chromosomes of seven species of _Prosimulium_ (Diptera : Simuliidae) from Alaska and British Columbia. Can. J. Zool. 40 : 1019-1033.

Basrur, V.R. and K.H. Rothfels. 1959. Triploidy in natural populations of the black fly _Cnephia mutata_ (Malloch). Can. J. Zool. 37 : 571-589.

Bennett, G.F. 1960. On some ornithophilic blood-sucking Diptera in

Algonquin Park, Ontario, Canada. Can. J. Zool. 38 : 377-389.

Bennett, G.F. 1961. On the specificity and transmission of some avian trypanosomes. Can. J. Zool. 39 : 17-33.

Bennett, G.F. 1963 (a). Use of P32 in the study of a population of Simulium rugglesi (Diptera : Simuliidae) in Algonquin Park, Ontario. Can. J. Zool. 41 : 831-840.

Bennett, G.F. 1963 (b). The salivary glands as an aid in the identification of some simuliids. Can. J. Zool. 41 : 947-952.

Bennett, G.F. and A.M. Fallis. 1960. Blood parasites of birds in Algonquin Park, Canada, and a discussion of their transmission. Can. J. Zool. 38 : 261-273.

Biggar, H.P. 1922. The works of Samuel de Champlain. The Champlain Soc., Toronto 1 : 1599-1607.

Biggar, H.P. 1925. The works of Samuel de Champlain. The Champlain Soc., Toronto 2 : 1608-1913.

Brett, W.J. 1955. Persistent diurnal rhythmicity in Drosophila emergence. Ann. ent. Soc. Amer. 48 : 119-131.

Brown, A.W.A. 1952. Rotary brush units for aerial spraying against mosquitoes and blackflies. J. econ. ent. 45 : 620-625.

Brown, A.W.A. 1960. Study tour of Simulium control in Africa. Wld. Hlth. Org./insecticides/119. 36 pp.

Brown, A.W.A. 1962. A survey of Simulium control in Africa. Bull. Wld. Hlth. Org. 27 : 511-527.

Brown, A.W.A., R.P. Thompson, C.R. Twinn and L.K. Cutkomp. 1951. Control of adult mosquitoes and blackflies by DDT sprays applied from aircraft. Mosquito News 11 : 75-84.

Cameron, A.E. 1918. Some blood sucking flies of Saskatchewan. Agric. Gaz. Can. 5 : 556-561.

Cameron, A.E. 1922. The morphology and biology of a Canadian cattle-infesting black fly. Can. Dept. Agric. Tech. Bull. 5 : 1-26.

Carlsson, G. 1962. Studies on Scandinavian black flies. Opusc. ent. supplementum. 21 : 279 pp.

Carlsson, G. 1966. Environmental factors influencing black fly populations. WHO/Oncho./66. 37.

Christophers, S.R. 1960. Aedes aegypti (Linn.). The yellow fever mosquito. Cambridge Univ. Press, Cambridge.

Clifford, M.F. (unpublished). Limnological characteristics of six Ozark streams. Personal communication.

Collins, D.L. and Jamnback, H. 1958. Ten years of black fly control in New York State. Proc. 10 Int. Congr. Ent. Montreal, 1956. 3 ; 813-818.

Coutant, C.C. 1964. Insecticide Sevin : effect of aerial spraying on drift of stream insects. Science 146 : 420-421.

Curtis, L.C. 1954. Observations on a black fly pest of cattle in British Columbia (Diptera : Simuliidae). Proc. ent. Soc. B.C. 51 : 3-6.

Dalmat, H.T. 1950. Studies on the flight range of certain Simuliidae

with the use of aniline marker. Ann. ent. Soc. Amer. 34 : 537-545.

Dalmat, H. T. 1951. Notes on Simuliidae (Diptera) of Guatemala including descriptions of three new species. Ann. ent. Soc. Amer. 44 : 31-58.

Dalmat, H. T. 1954. Ecology of simuliid vectors of Onchocerciasis in Guatemala. Amer. Midland Naturalist 52 : 175-196.

Dalmat, H. T. 1955. The black flies (Diptera : Simuliidae) of Guatemala and their role as vectors of Onchocerciasis. Smithson. misc. Coll. 125 : 1-425.

Davies, D. M. 1949. Variation in taxonomic characters of some Simuliidae (Diptera). Can. Ent. 81 : 18-21.

Davies, D. M. 1950. A study of the black flies population of a stream in Algonquin Park, Ontario. Trans. R. Can. Inst. 28 : 121-160.

Davies, D. M. 1951. Some observations on the number of black flies (Diptera : Simuliidae) landing on coloured clothes. Can. J. Zool. 29 : 65-70.

Davies, D. M. 1952. Population and activity of adult female black flies in a vicinity of a stream in Algonquin Park, Ontario. Can. J. Zool. 30 : 287-321.

Davies, D. M. 1953. Longevity of black flies in captivity. Can. J. Zool. 31 : 304-312.

Davies, D. M. 1957. Microsporidian infection in Ontario black flies. Proc. ent. Soc. Ont. 87 : 79.

Davies, D. M. 1958. Some parasites of Canadian black flies (Diptera :

Simuliidae). Proc. 15 Int. Cong. Zool. 660-661.

Davies, D.M. 1959. The parasitism of the black flies (Diptera : Simuliidae) by larval water mites of the genus Sperchon. Can. J. Zool. 37 : 353-369.

Davies, D.M. 1961. Colour affecting the landing of bloodsucking black flies on their host. Proc. ent. Soc. Ont. 91 : 267-268.

Davies, D.M., and B.V. Peterson. 1956. Observation on mating, feeding, ovarian development, and oviposition of adult black flies (Simuliidae : Diptera). Can. J. Zool. 34 : 615-655.

Davies, D.M. and B.V. Peterson. 1957. Black flies over lakes (Simuliidae : Diptera). Ann. ent. Soc. Amer. 50 : 512-514.

Davies, D.M. and P.D. Syme. 1958. Three new Ontario black flies of the genus Prosimulium (Diptera : Simuliidae). Can. Ent. 90 : 744-759.

Davies, D.M., B.V. Peterson, and D.M. Wood. 1962. The black flies of Ontario. Proc. ent. Soc. Ont. 92 : 71-154.

Davies, L. 1951. Some observations on Simuliidae (Diptera) at Halands Fjord, Norway. Oikos 3 : 193-199.

Davies, L. 1954. Observations on P. ursinum at Halands Fjord, Norway. Oikos 4 : 94-98.

Davies, L. 1955. Behaviour of young and old females of the black fly S. ornatum. Nature, Lond. 176 : 979-980.

Davies, L. 1957. A study of the black fly S. ornatum (Diptera) with

particular reference to its activity on grazing cattle. Bull. ent. Res. 48 : 407-424.

Davies, L. 1961 (a). Ecology of two Prosimulium species (Diptera) with reference to their ovarian cycles. Can. Ent. 93 : 1113-1140.

Davies, L. 1961 (b). Preliminary remarks on the structure of primitive Simuliidae and the probable affinities of the family with Chironomidae. Proc. R. ent. Soc. Lond. 26 : 13.

Davies, L. 1963. The seasonal and diurnal changes in the age composition of adult Simulium venustum Say populations near Ottawa. Can. Ent. 95 : 654-667.

Davies, L. 1965. On spermatophores in Simuliidae (Diptera). Proc. R. ent. Soc. Lond. 40 : 30-34.

Davies, L. and C.B. Williams. 1962. Studies on black flies (Diptera : Simuliidae) taken in a light trap in Scotland. Trans. R. ent. Soc. Lond. 114 : 1-20.

deCunha, A.B. 1960. Chromosomal variation and adaptation in insects. Ann. Rev. Ent. 5 : 85-110.

DeFoliart, G.R. 1951. A comparison of several repellents against black flies. J. Econ. ent. 44 : 265-266.

DeFoliart, G.R. and M.R. Rao. 1965. The ornithophilic black fly S. meridionale Riley (Diptera : Simuliidae) feeding on man during autumn. J. med. Ent. 2 : 84-85.

Doby, J.M., B. Rault and F. Saguez. 1965. Observations on the

nyctohemeral emergence rhythm of adult Simuliidae (Diptera) under laboratory conditions. WHO/Oncho./31-65.

Downe, A.E.R. 1957. Precipitin test studies on rate of digestion of blood meals in black flies (Diptera : Simuliidae). Can. J. Zool. 35 : 459-462.

Downe, A.E.R. and P.E. Morrison. 1957. Identification of blood meals of black flies (Diptera : Simuliidae) attacking farm animals. Mosquito News 17 : 37-40.

Downes, J.A. 1958 (a). Assembly and mating in the biting nematocera. Proc. 10th Int. Cong. Ent., Montreal, 1956. 2 : 425-434.

Downes, J.A. 1958 (b). The feeding habits of biting flies and their significance in classification. A. Rev. Ent. 3: 249-266.

Downes, J.A., A.E.R. Downe and L. Davies. 1962. Some aspects of the behaviour and physiology of biting flies that influence their role as vectors. Proc. 11 Int. Kongress Fur Entomologie, Wien 1960, 3 : 119-121.

Dumbleton, L.J. 1962 (a). Taxonomic characters in the pre-adult stages of Simuliidae (Diptera). N.Z. J. Sci. 5 : 496-506.

Dumbleton, L.J. 1962 (b). Aberrant head structure in larval Simuliidae. Pacific Insects 4 : 77-86.

Dumbleton, L.J. 1963. Evolution in some aquatic nematocera (Diptera). N.Z. Ent. 3 : 34-41.

Dunbar, R.W. 1958. The salivary gland chromosomes of two sibling

species of black flies included in E. aureum Fries. Can. J. Zool. 36 : 23-44.

Dunbar, R. W. 1959. The salivary gland chromosomes of seven forms of black flies included in Eusimulium aureum Fries. Can. J. Zool. 37 : 495-525.

Dyar, H. G. and R. C. Shannon. 1927. The North American two-winged flies of the family Simuliidae. Proc. U. S. Nat. Museum 69 : 1-54.

Eddy, S. and T. Surber. 1947. Northern fishes. Univ. Minnesota Press, Minneapolis. 12 + 276 pp. and 57 figs.

Edgar, S. A. 1953. A field study of the effect of black fly bites on egg production of laying hens. Poultry Sci. 32 : 779-780.

Edwards, F. W. 1915. On the British species of Simulium. Bull. ent. Res. 6 : 23-42.

Edwards, F. W. 1920. On the British species of Simulium. Bull. ent. Res. 11 : 211-246.

Emery, W. T. 1913. Morphology and biology of Simulium vittatum and its distribution in Kansas. Kansas Univ. Sci. Bull. 8 : 323-362.

Enderlein, G. 1930. Der heutige Stand der Klassification der Simuliiden. Arch. Klassif. Phylog. Ent. 1 : 77-97.

Fairchild, G. B. and E. A. Barreda. 1945. DDT as a larvicide against Simulium. J. econ. Ent. 38 : 694-699.

Fallis, A. M. 1964 (a). Protozoan life cycles : recent advances in parasitology. Amer. Inst. Biological Sci. Meeting of August 27, 1964.

Fallis, A.M. 1964 (b). Feeding and related behavior of female Simuliidae (Diptera). Experimental Parasitology 15 : 439-470.

Fallis, A.M. and G.F. Bennett. 1958. Transmission of Leucocytozoon bonasae Clark, to ruffed grouse (Bonasa umbellus Linn.) by black flies Simulium latipes Mg. and Simulium aureum Fries. Can. J. Zool. 36 : 533-539.

Fallis, A.M., D.M. Davies, and M.A. Vickers. 1951. Life history of Leucocytozoon simondi Mathis and Leger in natural and experimental infection and blood changes produced in the avian host. Can. J. Zool. 29 : 305-328.

Fallis, A.M., R.C. Anderson and G.F. Bennett. 1956. Further observations on the transmission and development of Leucucytozoon simondi. Can. J. Zool. 34 : 389-404.

Fassett, N.C. 1960. A manual of aquatic plants. Univ. Wisconsin Press, Madison. 7 + 405 pp.

Fredeen, F.J.H. 1958. Black flies (Diptera : Simuliidae) of the irrigated areas of Manitoba, Saskatchewan and Alberta. Proc. 10 Int. Cong. Ent. Montreal, 1956. 3 : 819-823.

Fredeen, F.J.H. 1959 (a). Rearing black flies in the laboratory (Diptera : Simuliidae). Can. Ent. 91 : 73-83.

Fredeen, F.J.H. 1959 (b). Collection, extraction, sterilization and low temperature storage of black fly eggs (Diptera : Simuliidae). Can. Ent. 91 : 450 : 453.

Fredeen, F.J.H. 1960. Bacteria as a source of food for black fly larvae. Nature, London 187 : 963.

Fredeen, F.J.H. 1961. A trap for studying the attacking behaviour of black flies, Simulium arcticum Mall. Can. Ent. 93 : 73-78.

Fredeen, F.J.H. 1963. Oviposition in relation to the accumulation of bloodthirsty black flies (Simulium (Gnus) arcticum Mall.) (Diptera) prior to a damaging outbreak. Nature, Lond. 200 : 1024.

Fredeen, F.J.H. 1964 (a). On the determination of the approximate age of a black fly (Diptera : Simuliidae) and its significance. Can. Ent. 96 : 109.

Fredeen, F.J.H. 1964 (b). Bacteria as food for black fly larvae (Diptera : Simuliidae) in laboratory cultures and in natural streams. Can. J. Zool. 42 : 527-548.

Fredeen, F.J.H. and J.A. Shemanchuck. 1960. Black flies (Diptera : Simuliidae) or irrigated systems in Saskatchewan and Alberta. Can. J. Zool. 38 : 723-735.

Fredeen, F.J.H., J.G. Rempel and A.P. Arnason. 1951. Egg laying habits, overwintering and life cycle of S. arcticum (Simuliidae : Diptera). Can. Ent. 83 : 73-76.

Fredeen, F.J.H., A.P. Arnason and B. Berck. 1953. Adsorption of DDT on suspended solids in river water and its role in black fly control. Nature, Lond. 171 : 700.

Fredeen, F.J.H., J.W.T. Spinks, J.R. Anderson, A.P. Arnason and

J.G. Rempel. 1953. Mass tagging of black flies (Diptera : Simuliidae) with radiophosphorous. Can. J. Zool. 31 : 1-15.

Franz, J.M. 1961. Biological control of pest insects in Europe. A. Rev. Ent. 6 : 183-200.

Forbes, S.A. 1912. On the black flies and buffalo gnats (Simulium) as possible carriers of pellagra in Illinois. Rep. Illinois State ent. 27 : 21-55.

Garnham, P.A. and J.P. McMahon. 1947. The eradication of Simulium neavei Roubaud from an Onchocerciasis area in Kenya colony. Bull. ent. Res. 37 : 619-628.

Garry, N. 1900. Diary of Nicholas Garry, Deputy Governor of Hudson Bay Company from 1822 to 1855. Trans. R. Soc. Can. 2 : 73-204.

Gjullin, C.M., H.F. Cross and K.H. Applewhite. 1950. Tests with DDT to control black fly larvae in Alaskan streams. J. econ. Ent. 43 : 696-697.

Gjullin, C.M., D.A. Sleeper and C.N. Husman. 1949 (a). Control of black fly larvae in Alaskan streams by aerial application of DDT. J. econ. Ent. 42 : 392.

Gjullin, C.M., O.B. Cope, B.F. Quisenberry and P.R. Duchanois. 1949 (b). The effects of some insecticides on black fly larvae in Alaskan streams. J. econ. Ent. 42 : 100-105.

Goulding, R.L. and C.C. Deonier. 1950. Observations on the control and ecology of black flies in Pennsylvania. J. econ. Ent. 43 : 702-704.

Grenier, P. and J. Rageau. 1960. Simulies (Diptera : Simuliidae) de Tahiti. Remarques sur la classification des Simuliidae. Bull. Soc. Pat. exot. 53 : 727-742.

Happold, D.C.D. 1965 (a). Mosquito ecology in central Alberta. I. Can. J. Zool. 43 : 795-819.

Happold, D.C.D. 1965 (b). Mosquito ecology in central Alberta. II. Can. J. Zool. 43 : 821-946.

Harker, J.E. 1961. Diurnal rhythm. A. Rev. Ent. 6 : 131-120.

Hasler, A.D. and J.E. Bardach. 1949. Daily migration of perch in lake Mendota, Wisconsin. J. Wildlife Management 13 : 11-14.

Hearle, E. 1932. The black flies of British Columbia (Simuliidae : Diptera). Proc. Ent. Soc. B.C. 29 : 5-18.

Hinton, H.E. 1958. The phylogeny of the Panorpoid orders. A. Rev. Ent. 3 ; 181-206.

Hitchen, C.S. and H.H. Goiny. 1966. Notes on the control of Simulium damnosum in the region of the Kainj dam project, northern Nigeria. WHO/Oncho./66 : 43.

Hocking, B. 1950. Further tests with insecticides against black flies (Diptera : Simuliidae) and a control procedure. Sci. Agric. 30 : 489-508.

Hocking, B. 1952. Protection from northern biting flies. Mosquito News 12 : 91-102.

Hocking, B. 1953. The intrinsic range and speed of flight of insects.

Trans. R. ent. Soc. Lond. 104 : 223-345.

Hocking, B. 1960. Northern biting flies. A. Rev. Ent. 5 : 135-152.

Hocking, B. and L.R. Pickering. 1954. Observations on the bionomics of some northern species of Simuliidae (Diptera). Can. J. Zool. 32 : 99-119.

Hocking, B. and W.R. Richards. 1952. Biology and control of Labrador black flies (Diptera : Simuliidae). Bull. ent. Res. 43 : 237-257.

Hocking, B., C.R. Twinn and W.C. McDuffie. 1949. A preliminary evaluation of some insecticides against immature stages of black flies (Diptera : Simuliidae). Sci. Agric. 29 : 69-80.

Hudson, A. 1963. Some features of the salivary glands of mosquitoes and other blood feeding insects. Can. J. Zool. 42 : 113-120.

Hutchinson, G.E. 1957. A treatise on limnology. Vol. 1. John Wiley and Sons, New York.

Ide, F.P. 1940. Quantitative determination of the insect fauna of rapid water. Publication Ont. Fish. Res. Laboratory 59 : University of Toronto Studies 47 : 1-20.

Jamnback, H. 1952. The importance of correct timing of larval treatments to control specific black flies (Simuliidae). Mosquito News 12 : 77-78.

Jamnback, H. 1956. An illustrated key to the black fly larvae commonly collected in New York State. N.Y. State Mus. Bull. 349, 10 pp.

Jamnback, H. 1962. An eclectic method of testing the effectiveness of

chemicals in killing blackfly larvae (Diptera : Simuliidae). Mosquito News 22 : 384-389.

Jamnback, H. 1964. Description of a trough testing technique useful in evaluating the effectiveness of chemicals as black fly larvicides. WHO/Oncho./28 : 64.

Jamnback, H. and D. L. Collins. 1955. The control of blackflies (Diptera: Simuliidae) in New York. N. Y. St. Mus. Bull. 350 : 3-113.

Jamnback, H. and H. S. Eabry. 1962. Effects of DDT, as used in black fly larval control, on stream Arthropods. J. econ. Ent. 55: 636-639.

Jobbins-Pomeroy, A. W. 1916. Notes on five North American buffalo gnats of the genus Simulium. Bull. U.S. Dep. Agric. 329 : 1-48.

Johannsen, O.A. 1903. Simuliidae. Bull. N.Y. State Mus. 68 : 336-388.

Jones, R.H. 1961. Some observations on biting flies attacking sheep. Mosquito News 21 : 113-115.

Kenton, E. 1925. The Jesuit relations and allied documents. McClelland and Stewart, Toronto. 22 pp.

Kindler, J. B. and F.R. Regan. 1949. Larvicide tests on black flies in New Hampshire. Mosquito News 2 : 108-112.

Knowlton, G. F. 1935. Simuliids annoy livestock. J. econ.. Ent. 28 : 1073.

Knowlton, G. F. and D.R. Maddock. 1944. Snipe flies in Utah. J. econ. ent. 37 : 119.

Krafchick, B. 1943. The mouthparts of blackflies, with species reference to Eusimulium lascivum Twinn. Ann. ent. Soc. Amer. 35 : 426-434.

Kutkuhn, J.H. 1958. Notes on the precision of numerical and volumetric plankton estimates from small sample concentrates. Dept. Zool. Ent. Iowa State Coll. J. 3250 : 11 pp.

Landau, R. 1962. Four forms of Simulium tuberosum (Lund.) in southern Ontario: a salivary gland chromosome study. Can. J. Zool. 40 : 921-939.

Lahontan, Baron de. 1703. Midges. A.C. McClury and Co. 1 : 68 pp.

Lea, A.O. and H.T. Dalmat. 1954. Screening studies of chemicals for larval control of black flies in Guatemala. J. econ. Ent. 47 : 135-141.

Lewis, D.J. 1950. Aspects of the structure, biology and study of S. damnosum. Ann. trop. med. Parasit. 51 : 340-358.

Lewis, D.J. 1958. The recognition of nulliparous and parous A. gambia by examining the ovary. Trans. R. Soc. Trop. med. Hyg. 52 : 456-461.

Lewis, D.J. 1960. Observations on S. damnosum in southern Cameroons and Liberia. Ann. trop. Med. Parasit. 54 : 208-223.

Lewis, T. and L.R. Taylor. 1965. Diurnal periodicity of flight by insects. Trans. R. ent. Soc. Lond. 116 : 393-479.

Linnaeus, C. 1758. Systema Naturae. 10 ed. Tomus 1.

Lugger, O. 1896. Buffalo-gnats, blackflies (Simuliidae). Univ.

Minnesota Agric. Expt. sta. ent. Div. Bull. 48 : 198-208.

Macan, T. T. 1962. Ecology of aquatic insects. A. Rev. Ent. 7 : 261-288.

Mackereth, F. J. H. 1963. Some methods of water analysis for limnologists. Freshwater Biology Association, Scientific Publication 21 : 70 pp. and 6 figs.

Mackerras, M. J. and I. M. Mackerras. 1948. Simuliidae (Diptera) from Queensland. Australian J. Sci. Res. 1 : 231-270.

Mackerras, M. J. and I. M. Mackerras. 1950. Notes on Australian Simuliidae (Diptera). Proc. Linn. Soc. N. S. W. 75 : 167-187.

Malloch, J. R. 1914. American black flies or buffalo gnats. U.S. Dept. Agric. Bur. Ent. Tech. Series B 26 : 1-72.

Marr, J. D. and D. J. Lewis. 1964. Observations on dry season survival of _S. damnosum_ Theobald in Ghana. Bull. ent. Res. 55 : 547-564.

McCombie, A. M. 1952. Factors influencing the growth of phytoplankton. J. Fish Res. Bd. 10 : 253-282.

McCrae, A. W. R. and M. A. Prentice. 1963. A new species of _Paracnephia_ Rubtzov (Diptera : Simuliidae) from Uganda. Proc. R. ent. Soc. Lond. 34 : 53-60.

McMahon, J. P. 1951. Discovery of early stages of _S. neavei_ in phoretic association with crabs and description of the pupa and male. Bull. ent. Res. 42 : 419-426.

McMahon, K. 1952. Phoretic association between Simuliidae and crabs.

Nature, Lond. 169 : 1018.

McMahon, S.P. 1957. DDT treatment of rivers for eradication of Simuliidae. Bull. Wld. Hlth. Org. 16 : 541-551.

McMahon, R.B., R.B. Highton and H. Goiny. 1958. The eradication of S. neavei from Kenya. Bull. WHO 19 : 75-107.

Metcalf, C.L. 1932 (a). Blackflies and other biting flies of the Adirondacks. N.Y. State Mus. Bull. 289 : 5-58.

Metcalf, C.L. 1932 (b). Control of biting flies in the Adirondacks. N. Y. State Mus. Bull. 289 : 59-72.

Metcalf, C.L. and W.E. Sanderson. 1931. Black flies, mosquitoes and punkies of the Adirondacks. N.Y. State Mus. Circular 5 : 1038.

Mortimer, C.H. 1952. Water movements in lakes during summer stratification. Evidence from the distribution of temperature in Windermere Lake. Phil. Trans. R. Soc. Lond. Series B. Biol. Sci. 236 : 355-404.

Muirhead-Thomson, R.C. 1957. Laboratory studies on the reactions of Simulium larvae to insecticides. Amer. J. Trop. Med. Hyg. 6 : 920-934.

Moss, E.H. 1955. The vegetation of Alberta. Botanical Rev. 21 : 493-567.

Moss, E.H. 1959. Flora of Alberta. Univ. Toronto Press, Toronto, vi + 546 pp.

Neel, L.K. 1951. Interrelation of certain physical and chemical features in a headwater limestone stream. Ecology 32 : 368-391.

Nicholson, H.P. 1945. The morphology of the mouth parts of the non-biting blackfly, Eusimulium dacotensis D. & S. as compared with those of the biting species, Simulium venustum Say (Diptera : Simuliidae). Ann. ent. Soc. Amer. 38 : 281-297.

Nicholson, H.P. and C.E. Mickel. 1950. The black flies of Minnesota. Univ. Minnesota Agric. Experimental Sta. Tech. Bull. 192 : 1-64.

Northcote, T.G. and P.A. Larkin. 1963. Limnology in North America. Univ. Wisconsin Press, Madison. 54 pp.

Odum, E.P. and A.D. de la Cruz. 1963. Detritus as a component of the ecosystem. AIBS Bull. 13 : 11-13.

Ogata, K. 1954. Studies on the diurnal rhythm of biting activity in S. venustum. Japanese J. Appl. Zool. 19 : 136-141.

O'Kane, W.C. 1926. Blackflies in New Hampshire. N.H. Agric. Exp. Sta. Tech. Bull. 32 : 1-23.

Osborn, H. 1896. Simuliidae : in insects affecting domestic animals. U.S. Dept. Agric. Div. Ent. Bull. 5 : 31-58.

Ovaza, M. 1961. Recent advances in knowledge on Simuliidae in the Ethiopian region with particular reference to species transmitting human Oncocerciasis. Wld. Hlth. Org. 2nd. Conf. on Onchocerciasis, Brazzaville.

Pacaud, A. 1942. Notes biologique sur une station de Simulium aureum

Fries aux environs de Paris. Bull. Biol. de la France et Belge. 76 : 226-238.

Palmen, E. 1958. Diel periodicity of pupal emergence in some north European chironomids. Proc. 10 Int. Cong. Ent. Montreal, 1956, 2 : 219-224.

Pasternak, J. 1963. Chromosome polymorphism in the black fly S. vittatum (Zett.). Can. J. Zool. 42 : 135-158.

Petersen, A. 1924. Bidrag til de Danske Simuliers naturhistorie. D. Kgl. Danska vid. Selsk. skr. Nat. Math. Afd. 8 : 237-341.

Peterson, B.V. 1955. A preliminary list of the black flies (Diptera : Simuliidae) of Utah. Proc. Utah. Acad. Sci. Arts Letters 32 : 113-115.

Peterson, B.V. 1956. Observations on the biology of Utah black flies (Diptera : Simuliidae). Can. Ent. 88 : 496-507.

Peterson, B.V. 1958. A rediscription of the female and first description of the male, pupa and larva of Prosimulium flaviatennus (S. & K.) with notes on the biology and distribution. Can. Ent. 90:469-473.

Peterson, B.V. 1959 (a). Observations on mating, feeding, and oviposition of some Utah species of black flies (Diptera : Simuliidae). Can. Ent. 91 : 147-155.

Peterson, B.V. 1959 (b). Notes on the biology of some species of Utah black flies (Diptera : Simuliidae). Mosquito News 19 : 86-90.

Peterson, B.V. 1960 (a). Notes on some natural enemies of Utah black

flies (Diptera : Simuliidae). Can. Ent. 92 : 266-274.

Peterson, B.V. 1960 (b). The Simuliidae (Diptera) of Utah. Great Basin Naturalist 20 : 81-104.

Peterson, B. V. 1962 (a). Observations on the mating swarms of S. venustum Say and S. vittatum Zett. (Diptera : Simuliidae). Proc. Ent. Soc. Ont. 92 : 188-190.

Peterson, B. V. 1962 (b). Cnephia abdita, a new black fly (Diptera : Simuliidae) from eastern North America. Can. Ent. 94 : 96-102.

Peterson, B. V. 1965. Lectotype designation for S. vittatum Zett. (Diptera : Simuliidae). Opuscula Entomologica 30 : 231-233.

Peterson, B. V. and D.M. Davies. 1960. Observations on some insect predators of black flies (Diptera : Simuliidae) of Algonquin Park, Ontario. Can. J. Zool. 38 : 9-18.

Peterson, B.V. and G.R. DeFoliart. 1960. Four new species of Prosimulium (Diptera : Simuliidae) from western United States. Can. Ent. 92 : 85-102.

Peterson, D.G. and A.S. Wolfe. 1958. The biology and control of the black flies (Diptera : Simuliidae) in Canada. Proc. 10 Int. Cong. Ent. Montreal, 1956, 3 : 551-564.

Peterson, D.G. and A.S. West. 1960. Control of adult black flies (Diptera : Simuliidae) in the forests of eastern Canada by aircraft. Can. Ent. 92 : 714-719.

Petrishcheva, P.A. and V.M. Saf'yanova. 1956. On the problem of the control of the larvae of black flies (Simuliidae). Zool. Zhur. 35 : 1849-1852. Summary from Rev. appl. Ent. (B) 47 : 63.

Phelps, R.J. and G.R. DeFoliart. 1964. Nematode parasitism of Simuliidae. Univ. Wisconsin Bull. 245 : 78 pp.

Phillipson, J. 1956. A study of factors determining the distribution of the larvae of the black fly, S. ornatum Mg. Bull. ent. Res. 47 : 227-238.

Phillipson, J. 1957. The effect of current speed in the distribution of the larvae of the black flies S. variegatum Mg. and S. monticola Fr. Bull. ent. Res. 48 : 811-819.

Prevost, G. 1947. Eradication of black fly larvae for a long term by the use of DDT at a critical time. Mimeograph Biol. Bur. Univ. Montreal. p. 7.

Puri, I.M. 1925 (a). On the life history and structure of the early stages of Simuliidae (Diptera : Nematocera). Parasitology 17 : 295-334.

Puri, I.M. 1925 (b). On the life history and structure of the early stages of Simuliidae (Diptera : Nematocera). Parasitology 17 : 335-369.

Puri, I.M. 1926. On the early stages of some of the Scandinavian species of Simulium (Simuliidae : Diptera). Parasitology 18 : 160-167.

Radzivilovskaya, A. 1950. Towards the ecology of the larvae and pupae of black flies (Simuliidae of the mountainous regions of the South U. Siran Taiga. Zool. Inst. Acad. Sci., U.S.S.R. 12 : 199-224.

Rawson, D.S. 1961. A critical analysis of the limnological variables used in assessing the productivity of Northern Saskatchewan lakes. Vei. Inst. Verim. Limn. 14 : 160-166.

Rempel, J.G. and A.P. Arnason. 1947. An account of three successive outbreaks of the black fly S. arcticum a serious livestock pest in Saskatchewan. Sci. Agric. 27 : 428-445.

Rempel, J.G., J.M. Naytor, K. Rothfels and B. Othoren. 1962. Sex chromosome constitutions of chironomid intersexes parasitized by nematodes. Can. J. genet. Cytology 4 : 92-96.

Riley, C.V. 1887. Simuliidae. In Report of the entomologist. Rep. Comm. Agric. 1886: 492-517.

Rothfels, K.H. 1956. Black flies : sibling, sex and species grouping. J. Heredity 47 : 113-123.

Rothfels, K.H. and R.W. Dunbar. 1953. The salivary gland chromosomes of the black fly S. vittatum Zett. Can. J. Zool. 3 : 226-241.

Rubtzov, I.A. 1939. On the migration of simuliid larvae. Mag. Parasit., Lenningrad 7 : 202-209.

Rubtzov, I.A. 1951. Contribution to the systematics of black flies (Simuliidae : Diptera) of central Asia. Trudy Zool. Inst. Kad. Nank. SSSP. T. 9 : 743-860.

Rubtzov, I.A. 1955. Variations in activity and blood sucking in connection with the gonotrophic cycle in Simuliidae. Trans. Zool. Inst. Acad. Sci. U.S.S.R. 21 : 353-364.

Rubtzov, I.A. 1956 (a). Nutrition and capacity for bloodsucking in black flies (Diptera : Simuliidae). Ent. Rev. 35 : 731-751.

Rubtzov, I.A. 1956 (b). Fauna of U.S.S.R. insekten (Diptera). Black flies (Simuliidae). Zool. Inst. Acad. Sci. U.S.S.R. 6 : 1-860.

Rubtzov, I.A. 1957. On the criteria of species in black flies (Family Simuliidae, Diptera). Zool. Zh. 36 ; 801-819.

Rubtzov, I.A. 1958. Gonotrophic cycle in blood sucking midges or gnats (black flies). Parasitological Symposium Zool. Inst. Acad. Sci. U.S.S.R. 18 : 255-282.

Rubtzov, I.A. 1959. Simuliidae (Melusinidae). In E. Linden, Die Fliegen der palaearktischen Region. p. 687 Stuttgart.

Rubtzov, I.A. 1962. Simuliid genera in the Ethiopian region. Zool. Zh. 41 : 1488-1502.

Rubtzov, I.A. 1964. Observations on mermithid nematodes parasitizing blackflies. WHO/EBL/19.

Rubtzov, I.A. and N.A. Vlasov. 1934. An experiment in applying emulsions for the control of blackflies. Rev. appl. ent (B.) 23 : 117.

Sagard, Brother Gabriel. 1632. Mosquitoes. The Champlain Soc., Toronto (1939). pp. 57-58, 63.

Sailer, R.I. 1953. The blackfly problem in Alaska. Mosquito News 13 : 232-235.

Say, T. 1823. Description of dipterous insects of the United States.

J. Acad. Nat. Sci. Phila. 3 : 28.

Shewell, G. E. 1952. New Canadian black flies (Diptera : Simuliidae). Can. Ent. 84 : 33-34.

Shewell, G. E. 1955. Identity of the black fly that attacks ducklings and goslings in Canada (Diptera : Simuliidae). Can. Ent. 87 : 345-349.

Shewell, G. E. 1958. Classification and distribution of arctic and subarctic Simuliidae. Proc. 10 Int. Congr. Ent. Montreal, 1956, 1 : 635-643.

Shewell, G. E. 1959. New Canadian black flies. Can. Ent. 91 : 83-87.

Shewell, G. E. and F. J. H. Fredeen. 1958. Two new species of black flies from Saskatchewan. Can. Ent. 90 : 723-738.

Slack, K. V. 1955. A study of the factors affecting the stream productivity by comparative methods. Investigations of Indiana lakes and streams. Dept. Zool. Univ. Indiana, 4 : 3-48.

Smart, J. 1934. Notes on the biology of Simulium pictipes. Can. Ent. 66 : 62-66.

Smart, J. 1944. The British Simuliidae, with keys to species. Scientific Publications of the Freshwater Biological Association of the British Empire 9 : 1-57.

Smart, J. 1945. The classification of Simuliidae (Diptera). Trans. R. ent. Soc. Lond. 95 : 463-532.

Sommerman, K. M. 1953. Identification of Alaskan black fly larvae. Proc. ent. Soc. Washington 55 : 258-273.

Sommerman, K. M. 1962. Notes on two species of Oreogeton predators on black fly larvae. Proc. ent. Soc. Washington 64 : 123-129.

Sommerman, K. M. 1964. Prosimulium esselbaughi sp. n., the Alaskan P. hirtipes. Proc. ent. Soc. Washington 66 : 141-145.

Sommerman, K. M., R. I. Sailer, and C. O. Esselbaugh. 1955. Biology of Alaskan black flies (Diptera : Simuliidae). Ecol. Monog. 25 : 345-385.

Stains, G. S. and G. F. Knowlton. 1940. Three new western Simuliidae (Diptera). Ann. ent. Soc. Amer. 33 : 77-80.

Stains, G. S. and G. F. Knowlton. 1943. A taxonomic and distributional study of Simuliidae of western United States. Am. ent. Soc. Amer. 36 : 259-280.

Steward, J. S. 1931. A note on Simulium species attacking horses and cattle in Herefordshire. Report of the Institute of Animal Pathology, Univ. Cambridge 2 : 194-197.

Stone, A. 1949. A new genus of Simuliidae from Alaska. Proc. ent. Soc. Washington 51 : 260-267.

Stone, A. 1952. The Simuliidae of Alaska. Proc. ent. Soc. Washington 54 : 69-96.

Stone, A. 1963. An annotated list of genus-group names of the family Simuliidae (Diptera). U. S. Dept. Agric. Tech. Bull. 1284 : 28 pp.

Stone, A. 1964. Guide to the insects of Connecticut. State Geological and Natural Resources Bull. 97 : 1-117.

Stone, A. and H.A. Jamnback. 1955. The black flies of New York State. N.Y. State Mus. Bull. 349 : 144 pp.

Strickland, E.H. 1911. Some parasites of Simulium larvae and their effects on the development of the host. Biol. Bull. 21 : 302-335.

Strickland, E.H. 1913. Further observations on the parasites of Simulium larvae. J. Morphol. 24 : 43-49.

Strickland, E.H. 1913. Some parasites of Simulium larvae and their possible economic value. Can. Ent. 45 : 405 : 414.

Strickland, E.H. 1938. An annotated list of the Diptera (flies) in Alberta. Can. J. Res. 16 : 175-219.

Strickland, E.H. 1946. An annotated list of the Diptera (flies) of Alberta. Can. J. Res. 24 : 157-173.

Syme, P.D. and D.M. Davies. 1958. Three new Ontario black flies of the genus Prosimulium (Diptera : Simuliidae). Can. Ent. 90 : 697-719.

Tarshis, I.B. 1965. A simple method for the collection of black fly larvae. Bull. Wildlife Disease Association 1 : 6-9.

Tarshis, I.B. 1965. Procurement and shipment of black fly eggs. Bull. Wildlife Disease Association 1 : 9-11.

Travis, B.V., D.L. Collins, G. DeFoliart and H. Jamnback. 1951. Strip spraying by helicopter to control black fly larvae. Mosquito News 11 : 95-98.

Travis, B.V. and D.P. Wilton. 1965. A progress report of simulated

stream tests of black fly larvicides. Mosquito News 25 : 112-118.

Truesdale, G.A., A.L. Downing and G.F. Lowden. 1955. The solubility of oxygen in pure and sea water. J. Appl. Chem. 5 : 53-62.

Twinn, C.R. 1936. The black flies of eastern Canada. Can. J. Res. 14 : 97-150.

Twinn, C.R. 1939. Notes on some parasites and predators of black flies (Diptera : Simuliidae). Can. Ent. 71 : 101-105.

Twinn, C.R. 1950. Studies of the biology and control of biting flies in northern Canada. J. Arctic Inst. N. Amer. 3 : 14-26.

Vargas, L. 1945. Simulidos del neuvo mundo. Inst. salubridad enferm. Trop. Mexico Monograph 1 : 1-241.

Wanson, M.L., L. Courtois and B. Lebied. 1949. L'eradication du Simulium damnosum (Theo.) a Leopoldville. Ann. Soc. Belge med. Trop. 29 : 373.

Wanson, M.L., L. Courtois and W. Bervoerts. 1950. L'extinction des Simulies de riviere a'Leopoldville. Ann. Soc. Belge med. Trop. 30 : 629.

Welch, H.E. 1962. New species of Gastromermis, Isomermis, and Mesomermis. (Nematode : Mermithidae) from black fly larvae Ann. ent. Soc. Amer. 55(5) : 535-542.

Welch, H.E. 1963. Mermithid parasites of black flies. Wld. Hlth. Org. Vector Control 57.

Wenk, P. 1963. Kopulation, Blutsaugen und Eiablage von B. erythrocephala

DeGeer (Diptera : Simuliidae) in laboratorium. Naturwissenschaften 11 : 409-411.

Wenk, P. 1965 (a). Über die Biologie blutsaugender Simuliiden (Diptera), Besamungstata der Femalebein Bluteubesuch und Anflud auf den Blutwirt. Z. Morph. Okol. Tiere 55 : 665-670.

Wenk, P. 1965 (b). Über die Biologie blutsaugender Simuliiden (Diptera). Z. Morph. Okol. Tiere 55 : 671-713.

Wenk, P. 1965 (c). The biology of blood-sucking Simuliidae (Diptera). WHO/Onch./66 : 36.

Wenk, P. and G. Schlorer. 1963. Wirtsorientierung und Kopulation bei blutsaugenden Simuliiden (Diptera). Zeitschrift fur Tropenmedizin und Parasitologie 14 : 177-191.

West, A.S., A.W.A. Brown and D.G. Peterson. 1960. Control of black fly larvae (Diptera : Simuliidae) in the forests of eastern Canada by aircraft spraying. Can. Ent. 42 : 745-754.

Williams, C.B. 1948. The Rothamsted light trap. Proc. R. ent. Soc. Lond. 23 : 80-85.

Williams, C.B. 1965. Black flies in a suction trap in the central highlands of Scotland. Proc. R. ent. Soc. Lond. 40 : 92-95.

Wilton, D.P. and B.V. Travis. 1965. An improved method for simulated stream tests of black fly larvicides. Mosquito News, 118-123.

Wolfe, L.S. and D.G. Peterson. 1958. A new method to estimate levels

of infestations of black fly larvae (Diptera : Simuliidae). Can. J. Zool. 36 : 863-867.

Wolfe, L.S. and D.G. Peterson. 1959. Black flies (Diptera : Simuliidae) of the forests of Quebec. Can. J. Zool. 37 : 137-159.

Wolfe, L.S. and D.G. Peterson. 1960. Diurnal behaviour and biting habits of black flies (Diptera : Simuliidae) in the forests of Quebec. Can. J. Zool. 38 : 489-497.

Wood, D.M. and D.M. Davies. 1965. The rearing of simuliids (Diptera). Proc. 12 Int. Congr. ent. London 1964, 2 : 822-823.

Wood, D.M., B.V. Peterson, D.M. Davies and H. Gyorokos. 1963. The black flies of Ontario. Proc. ent. Soc. Ont. 93 : 99-129.

Woodmanse, R.A. and B.J. Grantham. 1961. Diel vertical immigration of two zooplankters (Mesocyclops and Chaoborus) in the Mississippi lake. Ecology 42 : 619-628.

Wu, Y.F. 1931. A contribution to the biology of Simulium (Diptera). Michigan Acad. Sci. Arts Letters 13 : 543-599.

Yakuba, V.N. 1959. On the migration of black fly larvae (Diptera : Simuliidae). Rev. Ent. URSS 38 : 424-434. (Rev. appl. Ent. (1961) 49 : 195).

Zahar, A.R. 1951. Ecology and distribution of black flies in southeast Scotland. J. Anim. Ecol. 2 : 33-62.